Ecology, habitat preference, and conservation of Neotropical non-volant mammal communities in Costa Rica's Caribbean lowlands

By

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ABSTRACT

Biodiversity in the tropics is continually being threatened by anthropogenic disturbances such as habitat degradation and fragmentation. Unfortunately, conservation decisions and management of wildlife are difficult tasks to undertake without adequate scientific knowledge. In the tropics, little is known about the conservation value of secondary forests for mammals, the manner in which fragmentation can affect low-density populations, how mammalian assemblages have changed over time, and even some of the most basic ecology of organisms. Herein, I use multi-species and single-species approaches at different spatial scales to address these topics using the non-volant mammals in the Caribbean lowland rainforests of Costa Rica. I first tested the null hypothesis that primary and secondary forests have equivalent assemblages of non-volant mammals. I found no significant differences in the community composition of non-volant mammals in these two forest types. This community-based study led me to address the population biology of the collared peccary, one of the most common species in these faunal surveys. Using both my data and historical records, I established that this species has been greatly affected by anthropogenic disturbances in the area, and increased after the extirpation of white-lipped peccaries. My work at both the community and population level emphasized that the rodent communities in the Caribbean lowlands are at low densities, as represented by trap success. Fragmentation of tropical forests may therefore have particular consequences for mammalian communities. I thus performed a landscape level study with 15 fragments in Costa Rica's Caribbean lowlands. This work revealed that forest fragments showed differences in species diversity and relative abundance. Larger fragments (>9 km^2) had higher relative abundance for all species. I also focused on the population biology of two species, the spiny pocket mouse, *Heteromys desmarestianus* and the arboreal vesper mouse, *Nyctomys sumichrasti*. My work on the former species included molecular genetic studies which revealed that the

Caribbean lowlands have cryptic diversity that has not been previously explored. In overview, non-volant mammalian communities of the Caribbean lowlands represent a rich assemblage of organisms that are crucial to the health of tropical ecosystems. While anthropogenic disturbances are affecting these populations, a good understanding of the conservation value of secondary forests, how fragmentation can affect populations, and the ecology of organisms is crucial for making data-driven management and conservation decisions.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Tropical ecosystems support some of the highest biological diversity in the world, but have suffered from common anthropogenic disturbances that threaten the survival of many species and populations. Among these threats, habitat degradation and fragmentation pose extremely serious risks to biodiversity (Dobson et al. 1997). Though the effects of landscape change on ecosytems has been the focus of much research, the biological and physical effects are still poorly understood (Harrison and Bruna 1999, Fahrig 2003, Ewers and Didham 2007), and little is known about the conservation value of secondary forests (Gardner et al. 2007a, Wright and Muller-Landau 2006a, Wright and Muller-Landau 2006b). Few data are available to address many of these important conservation questions in the tropics, and particularly in Costa Rica's Caribbean lowlands, mainly because: 1) fewer studies have been conducted in comparison to temperate systems, 2) there has been a lack of standardized methodologies used in studies, and 3) the basic biology of many organisms is still poorly understood.

As conservation and management plans aim to attenuate the effects of anthropogenic disturbances on animal populations, it is imperative to first understand habitat preferences, behavioral patterns, factors affecting population fluctuations, and basic population parameters for species of interest. In addition, species assemblages and population changes should be explored with a strong historical component to fully comprehend the extent of change that has occurred and fully understand the evolutionary changes in these ecosystems. Understanding the efficiency of monitoring protocols and methodology is crucial to implementing management and conservation efforts. Only with a full understanding of the underlying assumptions of issues that may confound results, will population monitoring be successful for the long-term.

Study region

The Caribbean lowlands represent ~ 27% of the terrestrial landmass (~13,760 km^2) of Costa Rica (McClearn et al. in press). Annual rainfall can vary across this area, ranging from ~2.5–5 m. Precipitation is lower January–March, although seasonal changes are not as drastic as on the Pacific side (McClearn et al. in press). The mammalian fauna today is largely representative of the entire assemblage that was present at the time of European settlement, although small remnant populations of some species are of grave conservation concern (Timm 1994, McClearn et al. in press). The mammals present in this region typically have wide distributions and are characteristic of lowland, Neotropical forests. Few studies have focused on the ecology and conservation of non-volant mammals in the area, and consequently, we know little about this assemblage in these less-seasonal, tropical forests.

As is common throughout much of the tropics, habitat alteration of this area occurred largely during the late 20th century (Dobson et al. 1997); in the early 1950's the cover of the Caribbean lowlands consisted mostly of primary and older secondary forests (McClearn et al. in press). Periodic waves of colonization and deforestation affected the landscape of the Caribbean lowlands; from 1976 to 1996 the forest cover in Sarapiquí decreased from 55% (513 km^2) to 34% (313 km^2) and correspondingly the number of forest fragments increased from 537 to 1231 (Sánchez-Azofeifa et al. 1999).

Why study non-volant mammals?

Non-volant mammals play diverse and important roles in Neotropical forests. Mammals can act as predators of seeds, fruits, and other animals, and as important seed dispersers. Mammals can have large effects on the demography and composition of plants (Sánchez-Cordero and Fleming 1993, Brewer and Rejmanek 1999, Mangan and Adler 2002, DeMattia et al. 2006, Hanson and Brunsfeld 2006). Additionally, mammals can be both prey and predators in these systems, and thus important components of the complex interactions of tropical food webs. Costa Rica's Carribbean lowlands are surprisingly understudied for non-volant mammals, even at the well-studied La Selva Biological Station, where major faunal changes are occurring to several vertebrate communities (Sigel et al. 2006, Whitfield et al. 2007). For conservation efforts to be effective and properly managed, understanding the non-volant mammals of the area, and how to implement long-term methodologies to study this fauna, is imperative.

Present research

The focus of this dissertation has been to answer the following broad questions: 1) are secondary forests of conservation value to non-volant mammals?; 2) how do anthropogenic disturbances affect non-volant mammal communities, and has this assemblage changed over time?; 3) how can we properly survey non-volant mammals to produce high-quality, long-term datasets to further elucidate patterns of change?; 4) what patterns of reproduction do we observe in these less-seasonal forests?; and finally, 5) do the Caribbean lowlands contain any cryptic diversity?

I employed a variety of techniques, and targeted various species, to study these broad questions in Costa Rica's Caribbean lowlands and elucidate patterns of habitat preference, ecology, and conservation of Neotropical non-volant mammal communities. First, I used a community-based approach, at a relatively small-scale, to test if the community composition of non-volant mammals is similar in primary and secondary forests (Chapters 1 and 2). I then focused on a single species of local interest, collared peccaries (*Pecari tajacu*), to investigate population dynamics at small and large temporal scales that would provide insights on this species' biology in a broad, and historical context (Chapter 2). Additionally, I provided data on the suitability of strip-census techniques in studying these mammalian communities, and present recommendations for creating a standard methodology that can be used to create long-term, and comparable, datasets (Chapter 1 and Chapter 2). My work at both the community and population level showed that rodent densities in the area are quite low, and therefore, that these populations may be more susceptible to anthropogenic disturbances. Thus, via small mammal trapping, I explore patterns of habitat use for rodents throughout fragments in the Caribbean lowlands (Chapter 3), and I present data on the population biology and effects of forest fragmentation on rodent communities (Chapters 3 and 4). Finally, my work with these rodents includes molecular data that suggest that the Caribbean lowlands likely have cryptic diversity, with a currently unrecognized new species of rodent (Chapter 5). As a whole, this body of work illustrates an integrated approach to elucidating biological patterns and processes of non-volant mammals in tropical ecosystems, particularly in an applied conservation biology manner.

CHAPTER 1

NON-VOLANT MAMMALIAN POPULATIONS IN PRIMARY AND SECONDARY NEOTROPICAL RAINFORESTS AS REVEALED BY TRANSECT SURVEYS

Abstract

Secondary forests are becoming a prominent feature in Neotropical landscapes, yet little is known about the conservation value of secondary forests for non-volant mammalian communities. We performed a 20-month study using transect walks to survey the non-volant mammalian fauna in primary and secondary forests at La Selva Biological Station in the Caribbean lowlands of Costa Rica. We found that secondary forests can hold complex mammalian communities and no species exhibited habitat preferences between primary and secondary forest. Overall, few behavioral and group dynamic characteristics changed among forest types. Our research also allowed us to address methodological questions about transect walks and determine the effectiveness of this method. Monthly detection rates varied widely by species and likely reflected short-term changes in behavior rather than population fluctuations. Air temperature and rainfall were the factors most associated with monthly detections rates for various species. Small scale areas of higher and lower use were evident for several species. The time of morning in which transects were walked did not affect detection rates, and increasing the number of observers per trail did not affect number of sightings. We report current abundances for the most commonly observed species, and note a general pattern of lower densities in the Caribbean lowlands than elsewhere in the Neotropics. This research highlights that in less seasonal, evergreen forests climatic factors can still affect mammalian behavior. Overall, we found that secondary forests are of high conservation value, and transect walks are a suitable

methodology to sample many non-volant mammal species, and we present recommendations on how to sample properly to conduct rigorous and long-term studies.

Introduction

Tropical ecosystems support some of the highest biological diversity in the world, but have suffered from common anthropogenic disturbances that threaten the survival of many species and populations. Among these threats, high levels of deforestation and habitat degradation have caused exceptional loss of biodiversity (Mace et al. 2005), and remain serious risks to these ecosystems as forest cover continues to decrease (Dobson et al. 1997). Nevertheless, converted land, used as pastures or agricultural fields, is often left abandoned and allowed to regrow after being overworked (Nepstad et al. 1991). Consequently, secondary forests are becoming a dominant feature of tropical landscapes (Gardner et al. 2007a, Wright and Muller-Landau 2006a). Worldwide, tropical secondary forests are created at a rate of 9 million ha per year, account for ~ 40% of all forested areas (Brown and Lugo 1990), and have overtaken a sixth of primary forests that were deforested in the 1990's (Wright 2005). In fact, some countries will likely only have secondary forest cover in the future (Parry et al. 2007, Wright and Muller-Landau 2006a).

The value of secondary forests to aid in the biodiversity crisis has been a subject of debate among scientists (Gardner et al. 2007a, Wright and Muller-Landau 2006a, Wright and Muller-Landau 2006b). Disagreements about this controversial issue and our ability to predict trends of biodiversity loss in the tropics can be largely attributed to lack of data (Gardner et al. 2007a). Thus, it is necessary to understand the manner and extent to which fauna respond to these forest type differences, and how specific these responses are by taxon and locality.

Primary and secondary forests can vary in many ways for both abiotic and biotic factors, although the manner and extent to which they vary can be affected by the history of land use and the age of the secondary stand (Guariguata et al. 1997, Guariguata and Ostertag 2001). These forest differences include biomass (De Camargo et al. 1999, Hughes et al. 1999), composition, richness, and demography of plants (Ferreira 1999, Guariguata et al. 1997, Turner et al. 1997), liana and epiphyte characteristics (Barthlott et al. 2001, Letcher and Chazdon 2009a), nutrient stocks (Hughes et al. 1999, Johnson et al. 2001, Vitousek et al. 1989), and microclimates (Uhl and Kauffman 1990). Given these abiotic and floristic differences in primary and secondary forests, we also would expect to see faunal responses to vary across forest type. Overall, studies that have looked at multiple taxonomic groups, or that have compiled and studied published literature, have found that primary forests are invaluable for conservation efforts because they typically have higher species richness and have different community compositions than secondary forests (Barlow et al. 2007a, Blake and Loiselle 2001, Dunn 2004, Gardner et al. 2007a, Gibson et al. 2011, Parry et al. 2007, Pröhl 2002).

Some animal groups have been studied more than others and responses to forest type can vary. For example, birds are considered one of the most sensitive taxa and differences are often detected among the two forest types (Barlow et al. 2007a, Barlow et al. 2007b, Blake and Loiselle 2001, Dunn 2004, Gibson et al. 2011, Parry et al. 2007). Insects show mixed results (Barlow et al. 2007a, Dunn 2004, Eggleton et al. 1997, Eggleton et al. 1995, Gibson et al. 2011, Vulinec 2002) likely due to extremely disparate life strategies and metrics measured. Mammals as a whole also do not show clear patterns, however general trends are difficult to discern because most studies have focused on rodents and bats (Gibson et al. 2011), which are likely not representative of the responses for mammalian communities as a whole.

Mammals are a particularly important group to examine because they are integral components of Neotropical systems (Cuarón 2000) and play important roles in the complex interactions of tropical food webs as crucial predators and prey. Mammals are key post-dispersal seed predators of a large number of plants and can remove a significant proportion of seeds beneath parent trees or from large mammal scat, ultimately affecting plant demography and composition in these forests (Sánchez-Cordero and Fleming 1993, Brewer and Rejmanek 1999, Mangan and Adler 2002, DeMattia et al. 2006, Hanson and Brunsfeld 2006). Mammalian communities, abundances, and behaviors can be affected by food resources, which can be directly or indirectly related to floristic characteristics. Some mammal species, such as howler monkeys and agoutis, are known to be affected by forest quality (Jorge 2008, Senf 2009), in abundance and behavior.

Although we would predict differences in the community composition and behavior of mammals between primary and secondary forest, this might not always be true. For instance, land use history, the proximity to source populations, and the age of regeneration can often have strong impacts on the recovery rate of secondary forests, and ultimately shape their resemblance to primary forests (Guariguata et al. 1997, Guariguata and Ostertag 2001). Few studies have focused on medium to large non-volant mammal communities, which makes it difficult to understand their responses to forest regeneration (Dunn 2004, Gibson et al. 2011, Parry et al. 2007). These few studies have shown mixed results; some provide evidence for differences in community composition (Parry et al. 2007), whereas others show no differences among primary and secondary forests (Barlow et al. 2007a, Gibson et al. 2011). Yet, no one has investigated the manner in which these communities can differ by forest type in the Caribbean lowlands of Central America. The mammalian community in the Caribbean lowlands differs in the species composition and relative abundances from the more studied Amazonian communities. To have a more informed view of the ecological value of secondary forests and the generality of conclusions (e. g., are responses consistent throughout the tropics and for many taxa?), it is important to study the effect of forest type on medium to large mammals in diverse locations.

Finally, it is clear that the landscape in the tropics is continually changing. To discern the conservation value of secondary forest and ecological factors that shape communities, there is a need for long-term data and standardized methodologies that will make results comparable among sites, years, and taxa. Inconsistent methodologies are one reason why scientists have been unable to come to a consensus about the conservation value of regenerating forests (Gardner et al. 2007a, Barlow et al. 2007a). Additionally, identifying locations that can be surveyed in the future will provide robust datasets that will allow us to understand regeneration processes.

The objective of this study was to compare non-volant mammal communities in primary and secondary forest in the Caribbean lowlands of Costa Rica. We worked specifically at La Selva Biological Station which is representative of the less seasonal forests of the Caribbean lowlands that have not been studied, and because of the major role this field station plays in tropical ecology. Our first objective was to compare the community composition of medium and large mammals, species habitat preferences, and behavioral differences in primary and secondary forests. Our second main objective was to lay the groundwork for long-term surveys and address methodological issues so that cross-site studies and long-term data can be compared accurately, resulting in a broader understanding of these ecological and conservation issues. We specifically addressed issues of sampling effort, effects of population fluctuations on cross-site /year comparisons, and the degree to which variation in environmental factors or microhabitat alters detection. Further, we addressed whether the time of day, number of observers, or time sequence that trails were walked was important. Overall, our work allows us to compare mammalian abundances in Caribbean lowland forests to other Neotropical sites and to make recommendations about how to properly sample these mammalian communities, and factors that need to be considered in cross-site and yearly comparisons.

Methods

We collected data on 348 survey days from September 2005 to June 2007 by walking 5 transects at La Selva Biological Station (Fig. 1.1). La Selva (10˚26′ N, 83˚59′ W) is located in northeastern Costa Rica's Caribbean lowlands at the confluence of the Río Sarapiquí and Río Puerto Viejo. La Selva is just over 16 km^2 of primary forest, selectively logged primary forest, secondary successional forests, and abandoned pastures and plantations (McDade and Hartshorn 1994). Annual average rainfall is ~ 4 m, with precipitation peaks occurring June–August and October–November (McClearn et al. in press). La Selva is a well-protected site, with trained park guards who patrol the area, though evidence of illegal hunting is sometimes seen (Romero, pers. obs.). Most mammalian species at La Selva are of wide-spread distribution, and the mammalian community is typical of Neotropical rainforests (Timm 1994).

We walked transects on preexisting man-made trails. Transects traversed a variety of habitats including primary forest, secondary forests with differing land use histories, managed successional plots, the arboretum, and ecological reserve. Four transects (1–4) were walked during the morning, starting at ~ 0700 hr. Transect 5, which overlapped in areas with transect 1, was walked nocturnally starting at ~ 1900 hr (Fig. 1.1). We did not start surveys in heavy rainfall, and if there was heavy rainfall during a walk, the observer paused until conditions improved. We abandoned surveys if we could not finish the transect walk before 1100 hr or 2300 hr. We walked a total 981.7 hrs, surveying 1,052.36 km (848.36 km diurnally and 204 km nocturnally).

Only 1 observer walked transects, except for the last 5 months, when 2 observers walked diurnal transects together. We walked transects at ~ 1 km/hr searching for non-volant mammals. When a mammal was encountered, we recorded the species, location of sighting, time of sighting, perpendicular distance from animal to the trail, and if the mammal was first noticed by sight or hearing. For arboreal animals, we noted the distance from ground level. For social mammals we recorded each group as one encounter, and all data collected were based on the first sighted individual. Additionally, we recorded the number of individuals and group radius. All distances were visually estimated, and binoculars were used to confirm identifications. We used powerful flashlights during nocturnal surveys.

We calculated detection rates as number of sightings per km walked (DRKm) and number of sightings per hr walked (DRHr). To test if monthly DRKm and DRHr could be used interchangeably, we performed a correlation for the entire survey, the diurnal portion only, and the nocturnal portion only.

Primary and secondary forest—To test if community composition differed between primary and secondary forest, we calculated a monthly DRKm, based on the number of individuals seen for each species in both forest types, and used a Multi-response Permutation Procedure (MRPP) with Sørensen (Bray–Curtis) distance measure. This procedure was run in PC-ORD v. 5, following the recommendations of McCune and Grace (2002).

To test for habitat preferences between primary and secondary forest for diurnal data, we categorized each mammal sighting by forest type. We used GIS land use layers from the OTS La Selva Geographic Information Systems website (http://ots.ac.cr/index.php?option=com_wrapper&Itemid=352) to assign each sighting into 2 broad categories—primary forest (all primary forest and ecological reserves) and secondary forest (includes all secondary forest types). Trail 2 was omitted from the analysis because of its edge habitat. We performed Chi-square tests, with expected values standardized based on km walked in each forest type, to assess habitat preference for all sightings combined, and specifically for agoutis, spider monkeys, howler monkeys, white-faced capuchins, variegated squirrels, and red-tailed squirrels.

We used Mann–Whitney U tests to examine if group size and group radius differed in primary and secondary forest for monkey species and coatis. We included singletons in the analysis for group size, but excluded them when looking at group radius (i.e., we omitted zeros). Coatis were excluded from the group radius analysis because of insufficient of data.

We tested if perpendicular sighting distance for spider, howler, and white-faced capuchin monkeys, agoutis, coatis, red-tailed squirrels, and variegated squirrels differed in primary and secondary forest with Mann–Whitney U tests. Differences in the above ground height between primary and secondary forest were tested for the three monkey species, and the red-tailed and variegated squirrels via Mann–Whitney U tests. We tested if the height above ground for the three monkey species differed with a Kruskall–Wallace test.

We created species accumulation curves as a function of km walked in primary and secondary forest to assess if sampling was sufficient in each forest type. For each forest type, we randomized our survey days 100 times to avoid any bias in the results that might arise because of the particular order in which the surveys actually occurred. We then fitted a 2-parameter, exponential rise to maximum regression line in the form of $y = a(1-e^{bx})$, where a was forced to be the maximum number of species found, and we compared our simulated data to our actual data. To determine how these curves compared to each other, we took the simulated curves and extracted data points, such as km where the curve plateaus and number of species where this plateau occurs.

Methodological considerations—To determine if our sampling was sufficient for the overall survey, we created and visually inspected species accumulation curves for the entire survey (diurnal and nocturnal surveys combined), diurnal portion only, and nocturnal portion only as a function of km walked. Because we found spatial and daily heterogeneity in numbers seen, we randomized the survey days 100 times and fit a regression line as described above for species accumulation curves in primary and secondary forest.

To assess population trends through time, we graphed monthly DRKm for the entire survey, nocturnal portions only, and diurnal portions only, and performed Pearson correlations with monthly DRKm and time. Additionally, we graphically viewed monthly DRKm for agoutis, spider monkeys, howler monkeys, white-faced capuchins, kinkajous, variegated squirrels, and red-tailed squirrels to discern population patterns of these species.

We tested if environmental factors affected monthly DRKm by performing a stepwise linear regression with alpha-to-enter and alpha-to-remove equal to 0.15. Variables entered were mean daily rainfall (mm), air temperature (°C), maximum air temperature (°C), and minimum air temperature (°C) for the current and previous month. The stepwise linear regression was performed for the diurnal portion, nocturnal portion, and diurnal and nocturnal DRKm combined. Additionally, we explored how these variables affected DRKm for agoutis, spider monkeys, howler monkeys, white-faced capuchins, and kinkajous. Meteorological data used were from La Selva's weather station (http://www.ots.ac.cr/meteoro/default.php?pestacion=2).

To assess if there are areas of high or low use in La Selva, we broke each trail into 300-m segments. Within each of these segments, we calculated the probability of having at least one mammal encounter by dividing the number of days where at least one mammal was seen by the total number of days that segment was sampled. For each trail, we then looked at the probabilities for each segment to detect areas of high or low use. We repeated this same analysis for agoutis, spider monkeys, howler monkeys, and white-faced capuchins. To objectively assess areas of high or low use, we calculated a binomial cumulative probability for each category (mammals, agoutis, spider, howler, and white-faced capuchin monkeys). The binomial probability of success was the mean of the number of days where at least one sighting occurred over all survey days, for each category in each trail. Segments with probabilities lower than 5% of the cumulative binomial distribution were deemed areas of low use, whereas segments higher than 95% were deemed hotspots.

We used a Chi-square test with Yate's correction to determine if more mammals were first detected by sight (visual observation) or hearing (animal vocalizations, or noise). We tested this for the entire survey, diurnal surveys alone, and nocturnal surveys alone. Furthermore, we tested if agoutis, monkeys, and kinkajous were detected more via sight or hearing.

During the last 5 months of the survey, we increased the number of observers walking together on the diurnal trails to 2. To test if this increase in sampling effort affected DRKm, we performed a Mann–Whitney U test using DRKm for the 5 months prior to this increase in observers, and the 5 months after. We omitted data from January 2007, because halfway through this month the change occurred.

All diurnal surveys were started at ~ 0700 hr, and completed by 1100 hr. To test if time of day within this ~ 4 hr span (early morning versus late morning), affected mammal activity, and confounded our results (detection rates and identification of hotspots), we alternated the direction in which trails 1 and 3 were walked from January–August 2006. We calculated an average sunrise time for each month (www.timeanddate.com), and broke up the trails into an ‘early’ section and ‘late’ section. The ‘early’ section of the trails were defined as any portion of the trail walked between sunrise and 2:45 hrs after sunrise, while the ‘late’ portion was the area of the trail walked after sunrise + 3:15 hrs. This created a 30 min buffer in between ‘early’ and ‘late’ that was discarded for the analysis. We chose + 2:45 and + 3:15 hr after sunrise because it divided the trails into ‘early’ and ‘late’ sections that were somewhat similar in the amount of time walked. Thus, each survey day for trail 1 and 3 was broken up into an ‘early’ section and a ‘late’ section, and because these trails were walked in alternating directions ‘early’ and ‘late’ sections are on opposite ends of the transect for alternating days. We then counted the number of mammals seen in the ‘early’ and ‘late’ portion for each survey day and standardized the number of encounters by multiplying the number of mammal encounters in the section (early or late) in which more time was walked that day by the proportion of minutes walked in the shortest section to the longest section. We then performed Mann–Whitney U tests to compare, for each distinct trail, the standardized number of encounters in the same spatial area, but at different times (i.e., ‘early’ vs. ‘late’ in the same physical area).

We used Distance 6.0 (http://www.ruwpa.st-and.ac.uk/distance/) to estimate abundances for species with 18 or more sightings. For social mammals, we first checked that group size did not affect detection by performing correlations between distances and group size; none of these correlations were significant. We estimated the density of groups (any group was treated as 1 sighting) using mean perpendicular sighting distance for each species. Even solitary species were sometimes seen with juveniles or aggregated in the same area, thus we multiplied the group estimates from Distance by mean group size to calculate density of individuals.

Results

We had 846 sightings representing 25 species. Seventeen species were seen diurnally, while 13 species were detected nocturnally (Table 1.1). Five species were detected both diurnally and nocturnally. The most sighted species was the collared peccary (Chapter 2), followed by agoutis. Of the monkeys, we encountered spider monkeys most often, then howler monkeys, and lastly, white-faced capuchins. Kinkajous were the most sighted nocturnal species (Table 1.1). DRKm for the entire survey was 0.8039, with the diurnal DRKm = 0.8204, and the nocturnal DRKm = 0.7353. Monthly DRKm and DRHr for diurnal and nocturnal ($r = 0.943$, $P < 0.001$), only diurnal ($r = 0.964$, $P < 0.001$), and only nocturnal ($r = 0.938$, $P < 0.001$) surveys were highly correlated, and because the routes were walked at a rate of ~ 1 km/hour, essentially the same value.

Primary and secondary forest—MRPP showed no significant differences in the community composition of mammals in primary and secondary forest. The chance-corrected within-group agreement, *A* (the statistic describing the effect size independent of sample size), was 0.005, with $P = 0.234$ (McCune and Grace 2002). The overall number of sightings in primary and secondary forest did not differ ($\chi^2_1 = 0.807$, $P = 0.369$). No significant differences in the number of sightings between forest types were observed for agoutis ($\chi^2_1 = 0.819$, $P = 0.366$), spider monkeys ($\chi^2_1 = 1.169$, $P = 0.280$), howler monkeys ($\chi^2_1 = 2.065$, $P = 0.151$), white-faced capuchins ($\chi^2_1 = 1.229$, $P = 0.268$), red-tailed squirrels ($\chi^2_1 = 2.551$, $P = 0.110$), or variegated squirrels ($\chi^2_1 = 0.183$, $P = 0.669$).

Group size data can be seen in Table 1.2. Group size in primary and secondary forest differed marginally in spider monkeys ($U_{48, 28} = 1668$, $P = 0.0532$), and howlers ($U_{23, 28} = 694.5$, $P = 0.0692$), but not significantly in white-faced capuchins ($U_{33, 18} = 809$, $P = 0.3391$), or coatis ($U_{6, 9} = 61$, $P = 0.1047$). Mean group radius for howler monkeys was 12.65 m (median = 8 m, range = 0.25–100 m, $SE = 2.49$, $n = 47$), for spider monkeys 9.97 m (median = 7 m, range =

0.25–50 m, $SE = 1.33$, $n = 69$), for white-faced capuchins 19.15 m (median = 15 m, range = 2–75 m, $SE = 2.13$, $n = 48$), and for coatis 3.92 m (median = 4, range = 0.25–10 m, $SE = 0.920$, $n = 9$). Group radius was not significantly different in primary and secondary forest for howler monkeys ($U_{18, 18} = 303.5$, $P = 0.359$), spider monkeys ($U_{33, 26} = 1010.5$, $P = 0.760$), or white-faced capuchins ($U_{27, 17} = 646.5$, $P = 0.353$).

Perpendicular sighting distance from the trail was variable among species (Table 1.3), and not significantly different in primary and secondary forest for spider monkeys ($U_{48, 28} = 1729$, $P = 0.202$), howler monkeys ($U_{24, 29} = 551.5$, $P = 0.086$), white-faced capuchins ($U_{33, 10} = 946$, $P = 0.085$), agoutis ($U_{81, 51} = 5336.5$, $P = 0.817$), coatis ($U_{6, 9} = 50$, $P = 0.860$), red-tailed squirrels ($U_{24, 10} = 429.5$, $P = 0.734$), or variegated squirrels ($U_{11, 10} = 130$, $P = 0.550$) (Table 1.4). No difference was observed in perpendicular sighting distance between primary and secondary forest when all observation were pooled ($U_{354, 245} = 109391$, $P = 0.126$).

There was no significant difference in above ground height between primary and secondary forest for howler monkeys ($U_{24, 27} = 563$, $P = 0.254$), spider monkeys ($U_{48, 28} = 1797.5$, $P = 0.590$), capuchins ($U_{33, 18} = 922.5$, $P = 0.207$), red-tailed squirrels ($U_{46, 10} = 1345.5$, $P = 0.467$), or variegated squirrels ($U_{11, 10} = 99.5$, $P = 0.139$). Height above ground was significantly different between monkey species: howlers (mean = 23.17 m, median = 20 m, $SE = 1.24$, $n = 64$), spider (mean = 21.63 m, median = 20, $SE = 0.955$, $n = 91$), and white-faced capuchin monkeys (mean = 15.02 m , median = 12 m, $SE = 1.11$, $n = 56$) ($K_{64, 91, 56} = 106$, $P < 0.001$). There was no difference in height between red-tailed squirrels (mean = 4.71 m, median = 3 m, $SE = 0.785$, $n = 43$) and variegated squirrels (mean = 4.24 m , median = 1.5 m, $SE = 1.28$, $n = 26$) ($U_{43, 26} = 1642$, $P = 0.091$). Mean above ground height for kinkajous was 15.95 m (median = 15 m, range = 0–50 m, $SE = 1.23$, $n = 52$).

Both the primary and secondary forest surveys had 13 species with similar amount of sampling effort. The species accumulation curve for primary forest increased quickly, then started to slow at 11 species at ~ 92 km. Only 2 more species were added with a subsequent ~ 293 km, and the total of 13 species was observed at ~ 215 km (Fig. 1.2). The simulated species accumulation curves were aggregated into the regression curve of *number of spp.* $= 13(1-e^{-0.0172x})$ where x = km walked ($R^2 = 0.704$). While the regression closely mirrored the original results, it did not begin to plateau until ~ 144 km with 11.8 species, ~ 52 km more than the actual results. A similar trend is seen for secondary forest, where a rapid increase in the number of species seen is observed in the first 98 km, and only one more species was added with an extra ~ 192 km. The 13 species in secondary forest were seen by ~ 260 km (Fig. 1.2). Additionally, the regression curve was *number of spp.* $= 13(1-e^{-0.0187x})$ ($R^2 = 0.6539$). This curve also began to plateau at 144 km with 12.1 species, coincidentally the same as for the primary forest randomizations.

Methodological considerations—The species accumulation curve for the entire survey began to plateau at ~ 303 km of sampling effort. Two more species were added later at ~ 833 km and 935 km. The regression curve of randomized sampling days was *number of spp.* $= 25(1-e^{-0.0065x})$, with an $R^2 = 0.7735$. The regression does not plateau until ~ 350 km with 22.4 species.

Monthly DRKm were variable for diurnal surveys, ranging from 0.542–1.177, and nocturnal surveys, ranging from 0.083–2.0 (Fig. 1.3). Population trends show minor decreases in DRKm over time for the diurnal and nocturnal surveys combined ($r = -0.605$, $P = 0.005$), diurnal surveys alone ($r = -0.492$, $P = 0.028$), and nocturnal surveys alone ($r = -0.598$, $P = 0.005$). Species specific variation in monthly DRKm appeared more pronounced in some species (e.g., howler monkeys and the two squirrel species), while agoutis had variable, but more stable monthly DRKm, with a general negative trend through time (Fig. 1.3).

Diurnal DRKm was not associated significantly with any of the environmental factors tested, but was marginally related with the previous month's mean daily rainfall ($R^2 = 0.174$, $P = 0.068$, Diurnal DRKm = 0.630 + 0.0164 × previous month's rainfall in mm). Nocturnal DRKm was associated with the current month's mean daily air temperature ($R^2 = 0.256$, $P = 0.023$, Nocturnal DRKm = 8.74 – 0.319 × monthly mean daily air temperature °C), but no environmental factors of the previous month. DRKm for the diurnal and nocturnal surveys combined were not associated with any environmental factors of the current or previous month.

Agouti detection rate was associated with the current month's mean daily temperature ($R^2 = 0.248$, $P = 0.025$, Agouti DRKm = 0.00205 – 0.000074 × mean daily temperature (°C)). We found no associations for the previous month's environmental factors. Spider monkey DRKm's only association was with the previous month's rainfall ($R^2 = 0.236$, $P = 0.03$, Spider monkey DRKm = 0.00005 + 0.000005 × previous month's rainfall (mm)). White-faced capuchins showed a marginally significant association with previous month's rainfall also ($R^2 = 0.184$, $P = 0.059$), although the residuals were not normally distributed for this species and thus we have little ability to discern the level of confidence in this test (Anderson–Darling = 0.848, $P = 0.024$). Howler monkeys and kinkajous showed no associations with environmental factors for the current or previous month.

The probability of seeing a mammal within a particular 300-m segment of a trail is quite variable, ranging from 0.0339–0.4098 (Table 1.5). The degree of habitat use by mammals for a given trail can be quite variable, as trail 3, or fairly constant throughout, as trail 4. All species combined, agoutis, and monkeys also exhibited patterns of differential habitat use, by either having areas of low or high use (Table 1.5).

Species accumulation curves for diurnal and nocturnal survey showed a plateaued pattern. The diurnal survey leveled off at ~ 180 km, while the nocturnal survey leveled at ~ 50 km (Fig. 1.4). The regressions for diurnal and nocturnal were $number\ of\ spp. = 17(1\text{-}e^{-0.0067x})$, with an $R^2 = 0.589$ and $number\ of\ spp. = 13(1\text{-}e^{-0.0296x})$, with an $R^2 = 0.8435$, respectively. The diurnal regression plateaued at ~ 288 km with 14.5 species, where the nocturnal regression plateaued at ~ 90 km with 12.1 species.

Overall, we initially detected more mammals by sight than hearing ($\chi^2_1 = 25.22$, $P < 0.0001$). When we broke up the data into diurnal and nocturnal surveys, which sampled different species (Table 1.1), we visually detected more animals diurnally ($\chi^2_1 = 24.68$, $P < 0.0001$), whereas there was no statistical difference for nocturnal surveys ($\chi^2_1 = 1.26$, $P = 0.2617$). We detected monkeys as a group more by hearing ($\chi^2_1 = 13.8$, $P = 0.0002$) but there were specific differences. White-faced capuchins were detected more by hearing ($\chi^2_1 = 10.58$, $P = 0.0011$). Spider monkeys were marginally detected more by hearing ($\chi^2_1 = 3.82$, $P = 0.0506$), whereas howler monkeys ($\chi^2_1 = 0.98$, $P = 0.322$) were not detected significantly more by either method. Agoutis were detected more by sight ($\chi^2_1 = 45.82$, $P < 0.0001$), whereas kinkajous were detected more often by hearing ($\chi^2_1 = 6.26$, $P = 0.0123$).

The number of observers did not significantly affect DRKm ($U_{5,\,5} = 35$, $P = 0.1437$). For trail 1, the time of day did not significantly affect the number of mammal sightings in either of the ‘late’ versus ‘early’ pairings ($U_{14,\,13} = 221.0$, $P = 0.2315$; $U_{14,\,13} = 198$, $P = 0.942$). For trail 3, one ‘early’ versus ‘late’ pairing was significantly different ($U_{14,\,12} = 238.0$, $P = 0.0126$), and the other nearly so ($U_{14,\,12} = 152.5$, $P = 0.0641$). Abundance estimates for different species are reported in Table 1.6.

Discussion

Primary and secondary forest— Our results demonstrate that secondary forests can hold complex communities of non-volant mammals, and are of great conservation value. The community composition of non-volant mammals (excluding small rodents) did not differ between forest types, and no species-specific habitat preferences were detected. Many studies in tropical areas have found differences between animal species composition or richness in primary and secondary forests (Barlow et al. 2007b, Dunn 2004, Gibson et al. 2011, Parry et al. 2007), including a bird study conducted at La Selva in the 1980–90's. Throughout the tropics, we know little about how non-volant mammal communities respond to regenerating forests (Dunn 2004, Gibson et al. 2011, Parry et al. 2007), and this is particularly true of Central America's Caribbean lowlands. Previous studies on these taxa highlight that community responses can vary, and determining the conservation value of secondary forest is difficult (Barlow et al. 2007a, Gibson et al. 2011, Parry et al. 2007).

Our results may be due to secondary forests at La Selva having recovered without further, major anthropogenic disturbances, and/or because the majority of mammals sampled have relatively large home ranges and do not preferentially use one forest type. Primary and secondary forests can differ in a variety of ways from soil nutrient stocks (Johnson et al. 2001), to the composition, demography, and coverage of plants (Guariguata et al. 1997, Letcher and Chazdon 2009b), and the abundance, species richness, and sex ratios of many animals (Blake and Loiselle 2001, Gardner et al. 2007b, Pröhl 2002). In the Caribbean lowlands of Costa Rica, when land use has not been intensive, structural characteristics (Guariguata et al. 1997, Guariguata and Ostertag 2001) and above-ground plant biomass and species richness of secondary forest can quickly restore themselves (~21–30 yr), and become similar to primary forest (Letcher and Chazdon 2009). La Selva's secondary forests arose from different land use histories including abandoned pastures and plantations (Hartshorn and Hammel 1994), and most have been left to regenerate since ~ 1980's, although different 'ages' of secondary forest are found within the biological station. Yet, regeneration of tropical forests depends not only on age since abandonment, but also on a variety of landscape factors such as proximity to other forested areas (Chazdon et al. 2007). The ability of animal seed dispersers to move between primary and degraded forests can accelerate regeneration (Wunderle 1997), and La Selva's secondary forests likely benefited from being spatially continuous with primary forest habitat.

Our habitat preference results for specific species are not surprising. Agoutis often do well in degraded and fragmented forests (Jorge 2008), and studies in Costa Rica have shown howler, spider, and capuchin monkey densities to be similar in primary and secondary forests (Lindshield 2006, Weghorst 2007). Red-tailed and variegated squirrels are typically seen more often in secondary and more disturbed forests (Best 1995, Enders 1935, Heaney 1984), though proximity to primary forest can be important (Enders 1935). We found no preference between forest types for squirrels. Red-tailed squirrels have a specialized diet, where 73% is composed of 4 species (Glanz 1996), and habitat preference is likely linked to the availability of food items.

Behavioral and group responses of mammals provide important information about how animals cope with changes in the environment and the degree of plasticity in their behavior. Group size, group radius, perpendicular sighting distance, and height above ground (for arboreal mammals) are behavioral characteristics that may change across forest types. For example, group size and radius can be affected by predation risk (Roberts 1996), and differences in these variables may indicate that species are responding to forest type directly or indirectly. We found differences in some of these behaviors or group dynamics for collared peccaries (Chapter 2), but few for the species discussed here. Group size for spider and howler monkeys was the only significant variable, albeit marginally, among these forest types. Primary and secondary forest can differ in a multitude of ways, but secondary forests are often thought to offer fewer food resources for primates (Arroyo-Rodríguez et al. 2007, Pozo-Monty and Serio-Silva 2007, Senf 2009). Reported behavioral differences in primary and secondary forests for these monkey species and coatis include changes in diet, time spent resting and feeding, frequency of howling, and foraging patterns (Chaves et al. 2011, Panger et al. 2002, Senf 2009, Valenzuela and Ceballos 2000), though interestingly, interspecies interactions between these three primates do not differ by forest type (Senf 2009). These results support the hypothesis that La Selva's secondary forests have recovered to a level where some species (monkeys, agoutis, coatis, squirrels) no longer exhibit habitat preferences or behavioral changes. However, to more accurately assess potential behavioral changes in the group dynamics for these mammals, it may be best to follow groups that spend significant portions of their time in both forest types and see how particular groups change behavior in different forest types.

Although MRPP showed no significant differences in community composition between primary and secondary forest, species accumulation curves highlight that walking both forest types allowed us to observe more species. Each forest type reached 13 species, however, both forest types needed to be walked to observe all of the diurnal species encountered. Although these results seem counter to our general conclusions of few differences between forest type, there were some species that were detected once during the 2-year study. When the communities in both forest types are regarded as a whole, no significant differences were observed. Our species accumulation curves for primary and secondary forest plateaued, which suggests that our sampling was thorough, although we know that we did not detect all species known to be present in the area (Timm 1994). Additionally, these curves showed that the minimum amount of effort required to reach a relatively stable number of species in both forest types is not trivial (~ 100 km), and our randomizations show that it may even require more effort (~ 50 km more).

Methodological considerations—To study these mammalian communities and address questions across sites or with long-term data we first need to understand methodological issues so that results can be compared accurately. The methodology used in this study, a basic strip-census technique using predetermined trails, provides valuable data to assess a variety of biological questions. The advantages to using this technique are that it is easy to carry out and costs are relatively minimal, but not all species can be detected, which is particularly true for many carnivores, small rodents, and bats. In addition, the amount of effort needed to properly sample the area, and collect reliable data, is not trivial. The species accumulation curve for the entire survey highlights the minimum effort required to observe a relatively saturated level of diversity (~ 303 km), and our simulations suggest that, on average, more effort may be required (~ 350 km). This general trend is similar to the species accumulation curves for primary and secondary forest presented above. Additionally, even more sampling is needed to address questions on habitat choices and behavior, estimate abundances, and determine reliable detection rates, as is the case with collared peccaries (Chapter 2). Therefore, studies using transect walks to study mammalian communities should be thorough with their sampling, as quick surveys likely will not provide data that are representative of the community as a whole.

Our monthly detection rates show similar patterns over our 2-year study. A general trend of decreasing detection rates was found for diurnal, nocturnal, and combined surveys. Detection rates can be useful to compare relative abundances of animals, particularly for species that are difficult to observe frequently and estimate abundances with programs like Distance. Diurnal and nocturnal surveys sampled different assemblages of the non-volant mammal community. Only 5 species overlapped for diurnal and nocturnal surveys, and thus, these general declines detected in both surveys are not a result of sampling the same species. Of all species tested individually, only agoutis showed a general trend of decrease over time. Monthly DRKm for the survey can be influenced by the detection rates of the most prominent species—collared peccaries and agoutis (diurnal), and kinkajous (nocturnal). Still, the regressions show a stronger decrease overall than can be accounted for by a particular species. For example, for kinkajous alone, no statistically significant trends over time were found, whereas for the nocturnal survey, an overall decline illustrates that the most prominent nocturnal species did not fully drive this trend. Although changes were noted overall and for agoutis, abundances for species can vary greatly (Wright et al. 1999) and data on 2 years can be illustrative of the population dynamics of a species or a community, but are likely not representative of long-term trends (Glanz 1993).

Monthly detection rates were variable for the diurnal and nocturnal surveys, and for particular species. Monthly detection rates can fluctuate typically as a result of changes in abundance or changes in detectability due to environmental and/or behavioral modifications. Although environmental factors such as rainfall can change the habitat characteristics of an area and affect the visibility of animals, this is a more important issue in forests where seasonal changes are characterized by dramatic changes in vegetation. La Selva is an evergreen forest, and while changes in foliage and vegetation occur with seasonal changes, they are likely not altering the visibility of most medium-sized mammals in a significant way. Additionally, short-term monthly changes in detection rate are likely not a result of changing densities for most mammals sampled. For instance, monkey populations can experience rapid declines due to famine or disease, but cannot rebound as quickly due to reproductive constraints on gestation time and total reproductive output. Thus, the changes observed in monthly detection rates over the short-term, are likely representative of changes in behavior, such as movement and subgrouping activity, rather than changes in abundance. Again, these results highlight the importance of conducting surveys in a time frame that allows for critical information about population trends through time to be understood. This is particularly important when making cross-site comparisons because without knowledge on general population patterns, it is difficult to generalize conclusions and understand if the results are due to specific patterns observed or to the timing of the study.

Many studies have shown that climatic factors can affect movement patterns, time of activity, subgrouping tendencies, reproduction, and home range size, which can all impact the detectability of animals. Overall detection rates for diurnal surveys were not found to be closely associated with any of the environmental factors we tested, although they were marginally positively correlated with rainfall of the previous month. The only abiotic factor measured which affected monthly nocturnal DRKm was the current month's mean ambient temperature. When monthly detection rates for diurnal and nocturnal portions were combined, no environmental factors were significant.

In a species specific context, we found air temperature and previous month's rainfall to be significantly associated with agoutis, spider monkeys, and white-faced capuchins, respectively, although the association for white-faced capuchins was only marginally significant. Indeed, the behavioral plasticity of *Dasyprocta* and monkeys in relation to environmental factors has been documented. For example, agoutis are predominantly diurnal (Doran 1997, Dunbar 1992, Dunbar et al. 2009, Korstjens et al. 2006, Korstjens et al. 2010, Norris et al. 2010), but occasional nocturnal activity is associated with food availability, mean daily temperature, and full moons (Aliaga-Rossel 2004, Lambert et al. 2009). Additionally, diurnal activity patterns can vary in response to luminosity (Aliaga-Rossel 2004), rainfall (Smythe 1978), and food resources (Jorge and Peres 2005, Smythe 1978). Moreover, seasonality of food can also affect diet, caching and seed removal behaviors, home range size, and social activity, which can in turn affect detectability (Aliaga-Rossel et al. 2008, Haugaasen and Tuck Haugaasen 2010, Henry 1999, Tuck Haugaasen et al. 2010, Tuck Haugaasen et al. 2012). For primates, changes in activity patterns are often due to shifts in climatic variables (Doran 1997, Dunbar 1992, Dunbar 1998, Dunbar et al. 2009, Korstjens et al. 2006, Korstjens et al. 2010, Lehmann et al. 2007). Environmental factors such as humidity, clouds, and particularly rainfall and ambient temperatures affect a suite of behaviors in spider monkeys including the start and end of activity, times of peak activity, time spent resting, feeding, traveling, and the total time active (González-Zamora et al. 2011). For capuchins, the behavioral changes in dry forests are associated with daily peaks of heat and dryness, and in the dry season altogether, include more time resting, travelling shorter distances, and spending less time travelling (Campos and Fedigan 2009). Additionally, capuchin behavior is affected by heat stress and water availability; activity within home ranges becomes more centered around water sources in hot, dry areas (Campos and Fedigan 2009). Howler monkey activity patterns can change depending on the availability of food sources. Indeed, increased time spent feeding and travelling has been reported during the wet season in Costa Rica and Nicaragua (Chapman 1988, Williams-Guillén 2003), although at La Selva, activity and foraging patterns were not dependent on season (Stoner 1996). This suggests that La Selva's less seasonal environment, with milder fluctuations in food availability, may mitigate drastic changes in behavior. To further understand how behavior is affected, tracking of particular groups or species over time is required. Overall, these results show that climatic variables can affect the detection rates of species, probably by altering behavior and food resources. Consequently, comparative studies should aim to collect data in the same season, and be attuned to the fact that even small climatic differences can affect the detectability of these species. This context is particularly important to address in cross-site studies where the same seasons vary in climatic variables.

All species had areas of high or low use at small spatial scales. Some areas are likely hotspots due to the availability of food resources and shelter, and these environmental preferences are species specific. For example, for agoutis microhabitat characteristics and fruit availability are important in determining habitat use; agouti home ranges are often centered on important food sources (Aliaga-Rossel et al.2008), which can shift in seasonal environments (Silvius and Fragoso 2003). These areas of higher use are typically used to forage, and are strongly influenced by availability of fruiting trees, and dense areas of foliage or fallen logs (Silvius and Fragoso 2003).

For the primates, small scale habitat preferences were also detectable. Each monkey had segments, and groups of consecutive segments, where they were never observed (Table 1.5). Although single segments with 0 observations were not considered statistically different from expected, the pattern of consecutive zeros likely suggests further that there are areas of higher and lower use, although this was not explicitly tested. At La Selva, the density of the most preferred trees of howler monkeys was the most important factor for habitat selection (Stoner 1996). These results illustrate the importance of surveying trails across a variety of microhabitats representative of the general study area, as over or under-sampling small areas may lead to erroneous detection rates and estimates of abundance.

Our species accumulation curves show that we surveyed sufficiently, both diurnally and nocturnally. It is clear from our results that the diurnal and nocturnal mammal communities in the Caribbean lowland forests are quite distinct and show little overlap in species activity. We know that the observed differences in species seen nocturnally and diurnally are due to differences in these communities and not merely habitat differences because the nocturnal trail overlapped with portions of a diurnal trail (Fig. 1.1), and the majority of species seen at night are known to be nocturnal from natural history information (Reid 2009). To fully understand these complex assemblages, surveys need to be conducted both nocturnally and diurnally. The manner in which sightings occur (sight vs. hearing) can provide information about which animals may be overlooked if they are not active. Some animals are more amenable to being detected by sight or hearing, because of morphology or behavioral characteristics. However, our study differed from one in southwestern Costa Rica where spider monkeys were detected more by auditory cues, highlighting that in different forests, different cues may be important in locating mammals (Weghorst 2007). The number of observers walking the survey did not affect detection rates for the overall survey or in a species-specific context for collared peccaries (Chapter 2). We therefore recommend that surveys with more than one observer increase their effort by having them walk different trails on the same day.

Additionally, we report that the directionality in which the trails were walked did not affect the location where mammals were detected, and thus time of day (early or late morning) did not affect detection rates in particular locations. For many diurnal mammals, activity is typically higher after sunrise, decreases during the morning, and often is minimal by midday when ambient temperatures can be high. For these reasons, no surveys were conducted past 1100 hr, and our data show no biases in detection rates within the morning; however, studies on more seasonal forests, where environmental changes can be more pronounced in particular seasons, are needed before generalizing these conclusions.

This survey method has proven useful to study segments of the mammalian communities in the Neotropics, although it does have limitations. For example, our survey was unable to detect all of the mammalian species present at La Selva (Timm 1994). This is particularly true for more elusive species such as many carnivores (in particular felids), small rodents, and bats. Other methodologies such as camera traps, print and scat identification, and trapping and mist netting efforts are needed to fully understand the complex relationships of the mammalian fauna in the Caribbean lowlands.

Abundance and group size in the Caribbean lowlands—Abundance estimates for Neotropical mammals using strip-census techniques and the program Distance (http://www.ruwpa.st-and.ac.uk/distance/) are common, though few data exist on the densities of non-volant mammals in lowland, evergreen forests. Abundance estimates are critically important in a management and conservation context; population changes and declines over time can only be assessed if rigorous density estimates are known, and repeated surveys provide a feasible manner to measure changes over time. La Selva plays a major role in the study of tropical ecology and provides a great site to understand ecological and conservation issues. To address methodological issues, so that cross-site studies and long-term data can be compared accurately, an understanding of how the mammalian community of La Selva compares to other Neotropical sites is essential.

General trends about the mammalian communities of the Caribbean lowlands become apparent when compared to other Neotropical, mammalian communities. Densities overall appear to be lower, and groups are smaller or tend to disband more readily than reported elsewhere. Kinkajous, red-tailed squirrels, and variegated squirrels elsewhere have reported density estimates higher than those reported herein (Table 1.6). Drastic changes in the populations (10 fold increase in 6 years) of red-tailed squirrels can occur (Glanz 1996), and changes in abundance have been linked to crop failures that are hypothesized to affect reproductive output (Glanz 1996). Studies in BCI report that walking surveys underestimate abundances for squirrels (Glanz 1996). Still, our densities for squirrels are low compared to other line-transect derived estimates. All 3 monkey species and coatis have densities which are within the bounds of those reported in the literature, albeit on the lower end (Table 1.6). Other studies in the Caribbean lowlands for howler and spider monkeys support that densities in this area are lower (Lindshield 2006, Senf 2009, Stoner 1994). The agouti was the second most encountered diurnal mammal, and was the only animal where our estimate fell well within the reported ranges (Table 1.6). This suggests that lowland Caribbean forests likely support lower densities of mammals overall. This is surprising given that food availability is more constant throughout the year than in more seasonal tropical forests.

Based on few studies, group sizes of monkeys in the Caribbean lowlands appear to be smaller than in other areas, and may represent a higher propensity of groups to disband into subgroups (Lindshield 2006, Senf 2009, Stoner 1994). This could be attributed to either environmental factors or our ability to properly assess troop size. Group size is important to study because it can affect group dynamics, ultimately influencing reproduction (Fedigan et al. 1996).

Spider monkey troops can be large, but often break into small subgroups of 3–4 individuals (Fedigan and Baxter 1984). Local food availability and annual precipitation can affect subgroup size (Aureli et al. 2008, Korstjens et al. 2006, González-Zamora et al. 2011), though other evidence suggests that it does not change seasonally or because of food availability (Ramos-Fernandez 2001). Howler monkeys have the largest groups in habitats with consistent food sources, such as semievergreen forests (Chapman and Balcomb 1998). However, they also break into smaller foraging units (Leighton and Leighton 1982), depending on food availability (Senf 2009, Chapman 1989, Chapman 1990). We would expect to see large groups in the evergreen forests of La Selva, yet, our group size is much lower than typically reported (Table 1.2) and even a previous study at La Selva (11 ± 4 (Stoner 1994)). This suggests that strip-censuses may underestimate group size or actually provide estimates of subgroup size. Larger subgroups tend to be more spread apart, and occupy several tree crowns, making it difficult to count all individuals. On the other hand, group cohesiveness, a factor poorly understood in this species (Bezanson et al. 2008), could have changed at La Selva. White-faced capuchin group cohesiveness is much firmer, and they do not respond to environmental factors by forming subgroups (Chapman 1990). Changes in density can influence group size with increasing populations forming larger groups, and not simply more groups (Fedigan et al. 1996).

Concluding remarks and recommendations—Despite widespread concern over tropical deforestation and the high rates in which secondary forest are being created, we remain surprisingly ignorant of the degree to which faunal communities differ between primary and secondary forest. Our study takes a unique approach by sampling medium and large mammals via transect walks in Costa Rica's Caribbean lowlands and reveals that secondary forests can hold complex mammalian communities and be valuable forests in conservation efforts. In addition, our analyses of microhabitat preferences, methodological issues, and variation in detection due to population fluctuations and climatic variables, lead us to make the following recommendations for long term surveys that are essential for understanding and monitoring these dynamic communities: 1) Surveys should be thorough so that the minimum effort in the field allows for a saturated level of diversity to be seen (as can be tested via species accumulation curves) yet comprehensive enough to provide a broader understanding of abundance and population fluctuations; 2) When making comparisons, data should be from the same season, and special attention should be given to the possible confounding factors that climate may have on results from different sites or years; 3) Surveys should traverse a variety of habitats representative of the general area to ensure that areas of high or low use are not being over or under-sampled by chance; 4) To increase the amount of data, multiple surveyors should walk different transects simultaneously; 5) One should test how the directionality of walking and timing influences results (a hotspot may in reality be a "hot time"); 6) It is imperative to understand the characteristics of the mammalian community, and how they generally compare to other sites, to provide a comprehensive background that enables us to study how and why differences arise across sites. Overall, we believe that following these recommendations will create more robust and defensible datasets that will allow long-term and cross-site studies to be compared accurately, resulting in a better understanding of complex ecological and conservation issues.

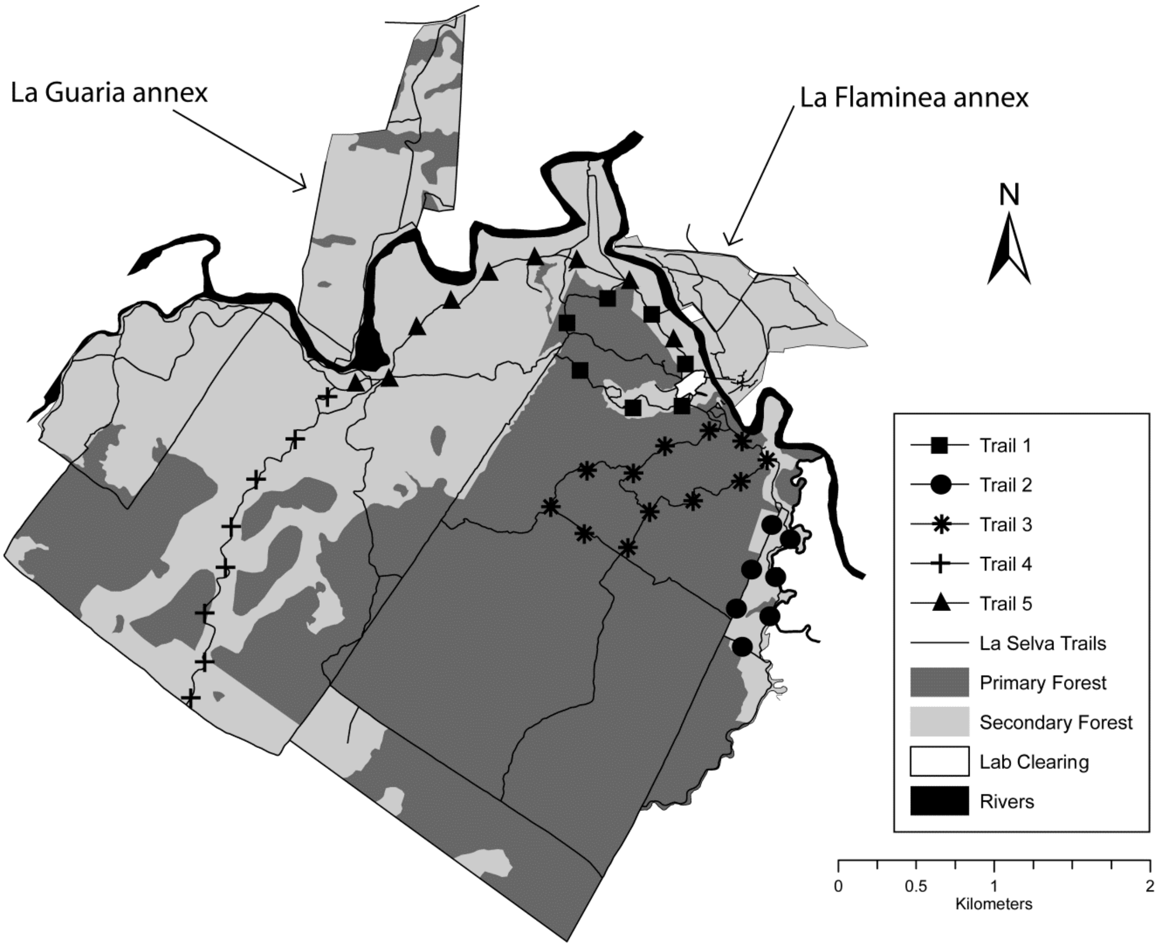

Figure 1.1—Map of La Selva Biological Station, in Sarapiquí, Costa Rica. Trails 1–4 were walked diurnally, and trail 5 nocturnally, for this study.

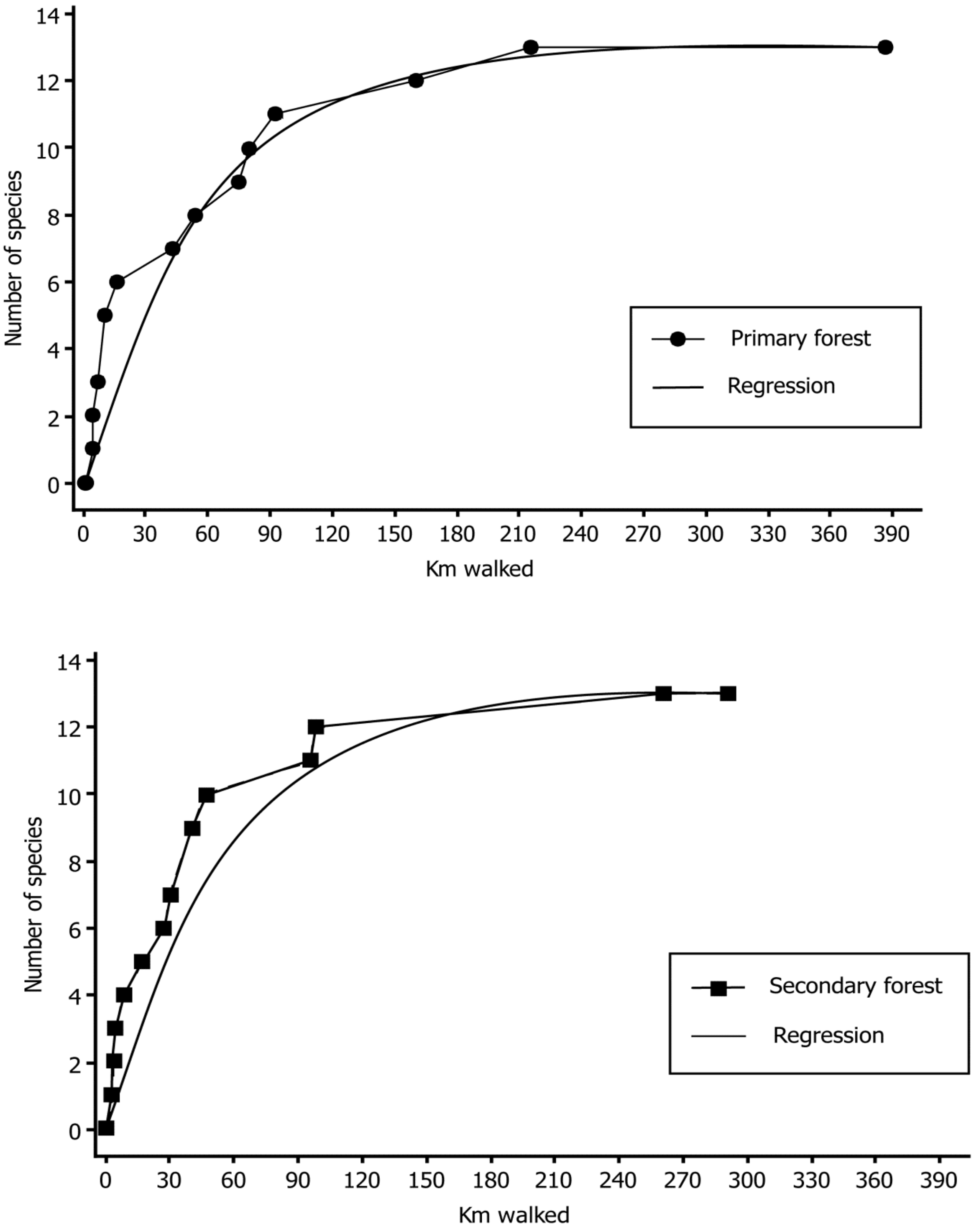

Figure 1.2—Species accumulation curves for primary forest and secondary forest.

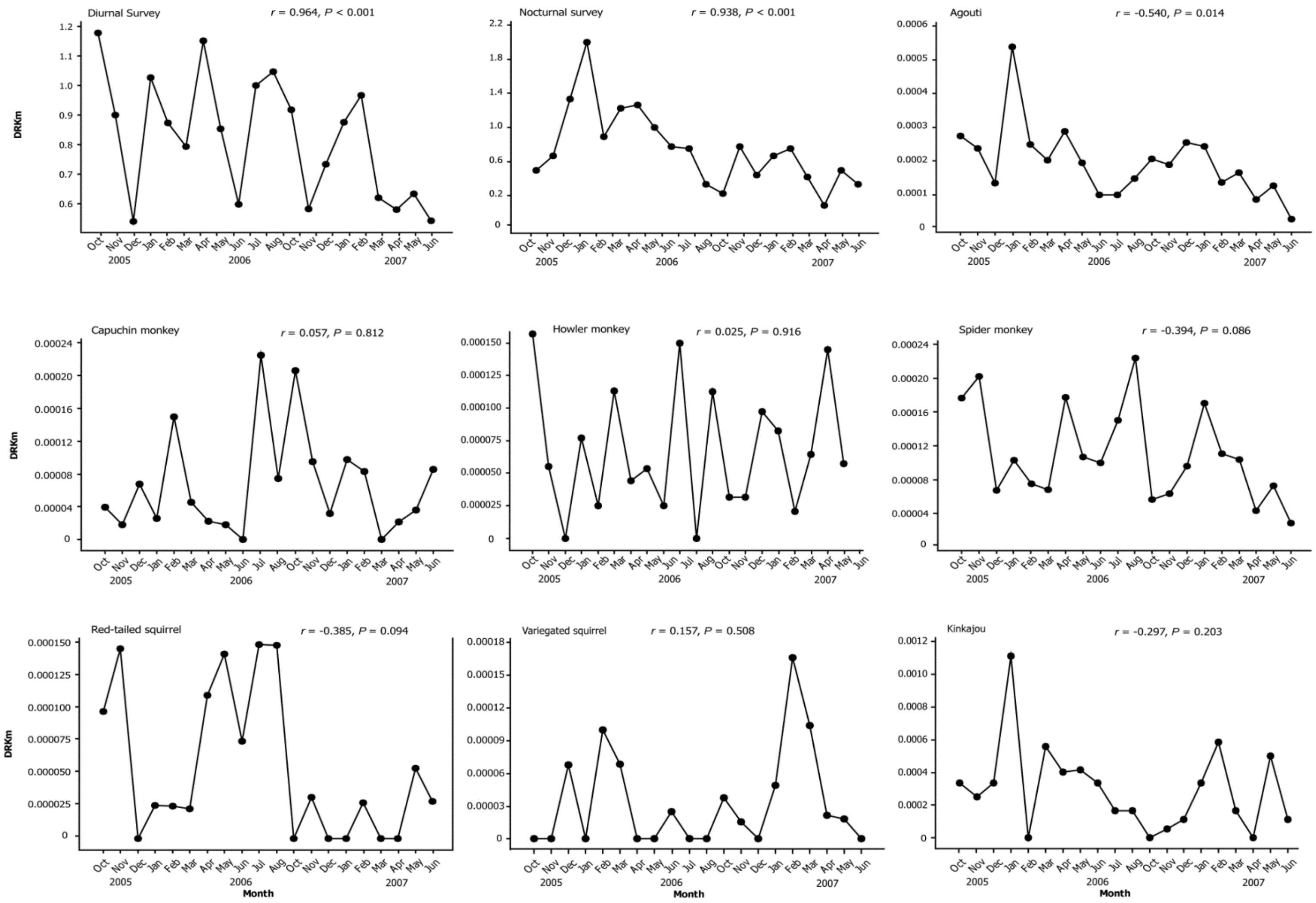

Figure 1.3—Monthly detection rates per km (DRKm) and correlations of monthly DRKm through time for the diurnal survey, nocturnal survey, and specific species. DRKm for species used diurnal data, except for the kinkajou (all nocturnal).

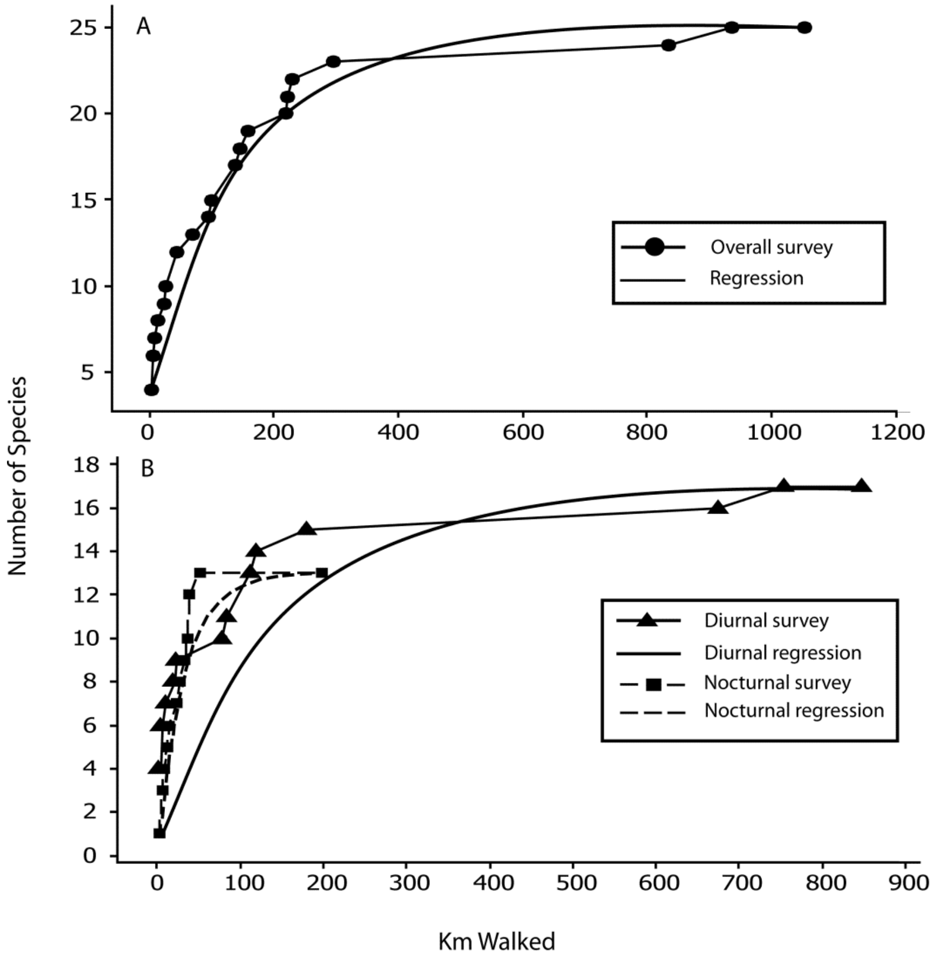

Figure 1.4—Species accumulation curve for (A) the entire survey, and (B) diurnal and nocturnal surveys separately.

Table 1.1—Detection rates per km for all species in the diurnal and nocturnal portions of the survey.

Species	Common name	Diurnal DRKm	Nocturnal DRKm
Alouatta palliata	Howler monkey	0.0731	0.0098
Choloepus hoffmanni	Two-toed sloth	0.0012	0.0294
Dasypus novemcinctus	Nine-banded armadillo	0.0059	0.1029
Pecari tajacu	Collared peccary	0.2558	0.0686
Tamandua mexicana	Tamandua	0.0071	0.0098
Unknown mammal		0.0035	0.0588
Ateles geoffroyi	Spider monkey	0.1073	0
Bradypus variegatus	Three-toed sloth	0.0024	0
Cebus capucinus	White-faced capuchin	0.0660	0
Chironectes minimus	Water opossum	0.0012	0
Coendou mexicanus	Porcupine	0.0012	0
Dasyprocta punctata	Agouti	0.1804	0
Eira barbara	Tayra	0.0024	0
Mazama americana	Red brocket	0.0012	0
Microsciurus alfari	Alfaro’s pygmy squirrel	0.0083	0
Nasua narica	Coati	0.0224	0
Sciurus granatensis	Red-tailed squirrel	0.0507	0
Sciurus variegatoides	Variegated squirrel	0.0307	0
Bassaricyon gabbii	Olingo	0	0.0294
Caluromys derbianus	Woolly opossum	0	0.0490
Cuniculus paca	Paca	0	0.0294
Didelphis marsupialis	Common opossum	0	0.0294
Marmosa zeledoni	Mouse opossum	0	0.0147
Philander opossum	Gray-four eyed opossum	0	0.0147
Potos flavus	Kinkajou	0	0.2549
Sylvilagus gabbi	Forest rabbit	0	0.0343

Table 1.2—Group size data for social animals. [1] indicates non-social species which were sometimes seen in groups (likely mothers with juveniles) and groups size was only used for density estimates and not behavioral analyses. Standard errors are in parentheses.

Species	Mean group size with singletons	Mean group size no singletons	Range	% singletons	Reported mean group size	Citations
Coati	3.222 (0.761) *n* = 18	5.44 (1.11) *n* = 9	1–10	50	2–26	Beisiegel 2001, Burger and Gochfeld 1992 Estrada et al. 1993, Kaufmann 1962, Glanz 1996, Gompper 1997, Gompper and Krinsley 1992
Howler Monkey	3.574 (0.305) *n* = 62	4.38 (0.322) *n* = 50	1–13	22	4.3–27.4	Bezanson et al. 2008, Chapman and Balcomb 1998 Cristóbal-Azakarte et al. 2005, Estrada 1982, Leighton and Leighton 1982
Spider Monkey	2.989 (0.193) *n* = 91	3.57 (0.199) *n* = 70	1–10	23	3.15–6.2	Weghorst 2007
White-faced Capuchin	5.357 (0.475) *n* = 56	5.98 (0.480) *n* = 49	1–15	13	9–14.4	Fedigan 1986, Pruetz and LaDuke 2001
Agouti[1]	1.107 (0.027) *n* = 153	—	—	—	—	—
Kinkajou[1]	1.137 (0.056) *n* = 52	—	—	—	—	—
Red-tailed Squirrel[1]	1.093 (0.056) *n* = 43	—	—	—	—	—
Variegated Squirrel[1]	1.039 (0.039) *n* = 26	—	—	—	—	—

Table 1.3—Perpendicular sighting distance statistics for all species with six or more sightings. Sample size is in parenthesis.

Species	Mean (m)	Median (m)	Range (m)	SE
Capuchin monkey	8.79 (56)	6	0–40	1.23
Paca	0.83 (6)	0	0–4	0.654
Howler monkey	14.29 (62)	10	0–100	2.12
Spider monkey	12.87 (91)	8	0–100	1.58
Olingo	8.33 (6)	6.5	0–23	3.45
Woolly opossum	2.75 (10)	2	0–8	0.958
Two-toed sloth	4.29 (7)	3	1.5–12	1.42
Agouti	3.18 (152)	1.75	0–35	0.371
Armadillo	2.56 (26)	2.5	0–8	0.428
Common opossum	1.08 (6)	0	0–4	0.712
Pygmy squirrel	2 (7)	2	0–5	0.681
Coati	5.03 (18)	2.5	0–27	1.74
Kinkajou	5.38 (52)	4	0–25	0.742
Red-tailed squirrel	3.59 (43)	2.5	0–10	0.453
Variegated squirrel	3.62 (26)	2.75	0–15	0.767
Forest Rabbit	2.29 (7)	2	0.5–5	0.576
Tamandua	2.13 (8)	1	0–7	0.934
Diurnal survey	6.44 (693)	4	0–100	0.415
Nocturnal survey	3.60 (144)	2	0–25	0.370

Table 1.4—Perpendicular sighting distance statistics between primary and secondary forest for six species and all observations (overall). Sample size is in parentheses.

	Primary forest				Secondary forest				
Species	Mean (m)	Median (m)	Range (m)	SE	Mean (m)	Median (m)	Range (m)	SE	*P*
Howler monkey	11.25 (24)	6.5	0–52	2.82	18.41 (27)	12	1–100	3.96	0.083
Spider monkey	10.7 (48)	6.5	0–50	1.75	16.04 (28)	10	0–100	3.75	0.202
Capuchin monkey	9.91 (33)	10	0–40	1.61	6.58 (18)	3.5	0–30	2.14	0.085
Agouti	3.201 (81)	2	0–25	0.426	4.010 (51)	3	0–35	0.836	0.817
Red-tailed squirrel	3.719 (24)	3	0.25–10	0.614	3.050 (10)	3	0–7	0.732	0.734
Variegated squirrel	3.864 (11)	4	0–8	0.65	4.5 (10)	2	0–15	1.74	0.550
Coati	7.42 (6)	3.25	0–27	4.27	4.67 (9)	3	0–19	2.02	0.860
Overall	5.922 (354)	4	0–52	0.423	7.502 (245)	3	0–100	0.939	0.126

Table 1.5—Probability of seeing at least 1 individual, in 1day, for a 300-m segment. (+) indicate segments with a significantly higher probability of detection compared to the average for the trail, whereas those marked (-) indicate significantly lower probabilities of detection.

Trail–segment	Mammal	Agouti	Spider monkey	Capuchin monkey	Howler monkey
1–1	0.4098(+)	0.1475(+)	0	0	0.0164
1–2	0.5410(+)	0.1967(+)	0.0820(+)	0.0164	0.0492
1–3	0.1967(-)	0(-)	0.0328	0	0.0328
1–4	0.4098(+)	0.0656	0.0656	0.0164	0.0492
1–5	0.2787	0.0328	0.0492	0	0.0656(+)
1–6	0.2787	0.0820	0	0.0328(+)	0
1–7	0.2787	0.0820	0.0656	0	0
1–8	0.1148(-)	0.0656	0.0328	0.0164	0
1–9	0.2295	0.1148	0	0.0164	0
2–1	0.1695	0.0509	0	0.0170	0.0170
2–2	0.2203(+)	0.0678	0.0509	0	0.0170
2–3	0.2203(+)	0.1186(+)	0.0678(+)	0	0
2–4	0.1356	0.0170	0.0339	0.0339(+)	0.0339
2–5	0.0848	0	0.0170	0.0170	0.0509
2–6	0.1017	0	0.0170	0.0170	0.0170
2–7	0.0848	0	0.0170	0	0.0170
3–1	0.2712(+)	0.1695(+)	0.0339	0.0339	0
3–2	0.1695	0.0508	0	0.1017(+)	0
3–3	0.2373	0.0847	0	0.0339	0.0169
3–4	0.2373	0.0508	0.0339	0	0.0169
3–5	0.0508(-)	0	0	0.0169	0.0169
3–6	0.0339(-)	0	0.0169	0	0
3–7	0.1525	0	0.0169	0.0508	0.0169
3–8	0.0847	0.0339	0	0.0169	0
3–9	0.1695	0.0678	0.0339	0.0508	0.0169
3–10	0.1017	0.0169	0.0169	0.0339	0
3–11	0.2373	0.0169	0.0678(+)	0.0169	0.0169
3–12	0.1695	0.0678	0.0339	0.0169	0.0339(+)
3–13	0.3220(+)	0.0847	0.0508(+)	0.0169	0.0339(+)
4–1	0.1698	0.0189	0.0943(+)	0.0377	0.0377
4–2	0.1698	0	0.0566	0.0755(+)	0.0377
4–3	0.1509	0.0189	0.0189	0	0.0377
4–4	0.1509	0	0.0566	0	0.0566
4–5	0.1698	0.0189	0.0566	0.0189	0.0566
4–6	0.1698	0	0.0377	0.0377	0.0189
4–7	0.1887	0	0.0189	0.0566	0.0189
4–8	0.0755(-)	0	0	0.0189	0.0189
4–9	0.0943	0.0189	0	0.0189	0.0189

Table 1.6—Density estimates, with standard errors in parentheses.

Species	Density (groups/km^2)	Density (individuals /km^2)	Reported densities (individuals /km^2)	Citations
Agouti	34 (3.07)	37.7 (3.5)	1–84	Cant 1977, Jorge 2008, Jorge and Peres 2005, Peres et al. 1997, Silvius and Fragoso 2003, Smythe 1978, Wright et al. 1994
Coati	1.99 (0.91)	6.4 (3.2)	1–70	Glanz 1993, McCoy 1984, Valenzuela 1998, Vaughan and Kaufmann 1962
Howler Monkey	2.8 (0.38)	9.8 (1.6)	5–>1000	Estrada 1982, Senf 2009, Stoner 1994,
Kinkajou	5.91 (0.78)	6.72 (0.95)	12.5–74	Estrada and Coates-Estrada 1985, Ford and Hoffmann 1988, Walker and Cant 1977
Red-tailed Squirrel	6.89 (0.96)	7.5 (1.1)	33–500	August 1981, Eisenberg et al. 1979, Glanz 1996, Heaney and Thorington 1978, O'Connell 1981
Spider Monkey	4.41 (0.49)	13.2 (1.7)	0.22–89.5	Lindshield 2006, Senf 2009 Weghorst 2007
Variegated Squirrel	4.08 (0.96)	4.2 (1.01)	7.8–300	Glanz 1996, Timock and Vaughan 2002, Vaughan and McCoy 1984
White-faced Capuchin	3.7 (0.50)	19.7 (3.2)	3.7–94	Senf 2009

CHAPTER 2

GROUP DYNAMICS, BEHAVIOR, AND CURRENT AND HISTORICAL ABUNDANCE OF PECCARIES IN COSTA RICA'S CARIBBEAN LOWLANDS

Abstract

The abundances and habitat preferences of peccaries in Neotropical forests are important to understand because these keystone species influence many aspects of the ecosystem. In the Caribbean lowlands of Costa Rica, we conducted walking surveys for ~ 2 years to study the behavior and population trends of collared peccaries (*Pecari tajacu*), and found that peccaries are abundant at La Selva Biological Station and detection rates were relatively constant through time. A stable estimate of detection rates was achieved only after 7–9 months of surveying. We found no habitat preferences between primary and secondary forest, yet there were some differences in group dynamics—group radius was larger and sighting distance was greater in primary forest while the number of singletons was higher in secondary forest. More peccaries were seen closer to the laboratory clearing, for a variety of probable reasons: habituation to humans, lower predation and hunting pressure, and various environmental/habitat factors. Peccary groups had spatially clumped distributions across the landscape and were more active diurnally than nocturnally. Collared peccary densities are relatively high compared to other Neotropical sites, with the exception of Barro Colorado Island. Collared peccaries have likely increased in abundance at La Selva, seemingly a few years after the extirpation of white-lipped peccaries (*Tayassu pecari*), which were abundant in the area 40–50 years ago. An understanding of the group dynamics, behavior, and habitat preference of collared peccaries is essential for management decisions and conservation efforts. Additionally, assessment of population changes should be carefully considered in a historical context, with a particular focus on how the

populations of the 2 peccary species have changed, and how these species might differentially affect their environment.

Introduction

Ungulates can have large impacts on ecosystems, affecting nutrient cycling and the composition of plant and animal communities (Augustine and McNaughton 1998; Bodmer 1991; Cullen et al. 2001; Hobbs 1996; Rooney and Waller 2003). The manner and extent to which ungulate populations respond to environmental changes are complex, not easy to discern, and often species-specific (Laurance et al. 2008, van Beest et al. 2012). Ungulate populations worldwide are susceptible to anthropogenic disturbances (Laliberte and Ripple 2004, Peres 2001). In the Neotropics, where ecosystems are experiencing major faunal changes (Daily et al. 2003; Sigel et al. 2006; Whitfield et al. 2007), historical and current data for most ungulate species are lacking. An example is the abundance of 2 peccary species, the white-lipped (*Tayassu pecari*) and collared (*Pecari tajacu*) peccaries of the Caribbean lowlands of Costa Rica.

Peccaries are ecologically important because they act as ecosystem engineers (Beck et al. 2010; Keuroghlian and Eaton 2009), modify plant diversity and composition by trampling seedlings (Beck 2007), and act as seed predators (Beck and Terborgh 2002; Bodmer 1991; Kuprewicz and García-Robledo 2010) and seed dispersers (Beck 2006; Keuroghlian and Eaton 2009; Lazure et al. 2010). Peccaries consume a wide variety of food items throughout their range, but in the tropics they primarily eat fruits, seeds (especially palms), pulp, roots, tubers, and occasionally animals (Altrichter et al. 2001; Barreto et al. 1997; Beck 2006; Kiltie 1981; Olmos 1993). Additionally, peccaries are important prey items for large carnivores, especially jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Garla et al. 2001; Harveson et al. 2000; Novack et al. 2005; Weckel et al. 2006a, 2006b).

Historically, collared and white-lipped peccaries shared much of their ranges; however, white-lipped peccaries have suffered severe population declines due to anthropogenic factors, especially overhunting (Chiarello 1999; Cullen et al. 2000; Peres 1996). Collared peccaries are also susceptible to human disturbances, although they are more resilient than white-lipped peccaries (Altrichter and Boaglio 2004; Cullen et al. 2000). Both peccary species represent a large proportion and biomass of hunted animals throughout their ranges (Alvardo et al. 1997; Bonaudo et al. 2005; De Souza-Mazurek et al. 2000; Roldán and Simonetti 2001; Wright et al. 2000). In areas where collared and white-lipped peccaries co-occur, white-lipped peccaries may outcompete collared peccaries (Altrichter and Boaglio 2004; Keuroghlian et al. 2004; Mendes Pontes and Chivers 2007). Although behavioral and morphological differences cause niche differentiation between these species (Desbiez et al. 2009; Kiltie 1982), ecologically the 2 species probably have similar impacts on forests.

Peccaries present interesting challenges as study subjects. Standard methods to estimate population densities are difficult to apply because it is hard to determine group size, and individuals have no unique identifying markings. Estimating densities is particularly complicated in tropical, non-deciduous forests, where a dense understory could reduce visibility.

Although much research has been done on peccaries, many aspects of their ecology in the tropics are still poorly understood. The biology of collared peccaries in the tropics is not the same as in arid areas because of well-known dietary and behavioral differences. In particular, there are few data on peccaries in the Caribbean lowlands of Central America. Peccaries in this area have suffered from increased hunting pressure and habitat change, as in many other areas of the Neotropics. White-lipped peccaries still persist in remote areas of the Caribbean lowlands, but have been locally extirpated from the majority of their historical range. In Costa Rica's Caribbean lowlands, La Selva Biological Station provides an excellent opportunity to study collared peccaries. At La Selva, collared peccaries are commonly observed, are relatively well protected, and have become a species of broad interest to scientists, local residents, ecotourists, and educators. Collared peccaries are generally perceived to have increased in density in recent years, to the extent that they may be negatively impacting the forest (Michel and Sherry 2012). A debate about managing peccary populations has arisen, but little historical data exist to assess long-term changes quantitatively.

We have observed and surveyed collared peccaries at La Selva for a number of years and herein combine our data with a review of the historical literature to form a broader picture of peccary biology and impact in the Caribbean lowlands. The aims of this paper are to: 1) elucidate population trends and detection rates of collared peccaries, 2) evaluate the efficacy of sampling via line-transects, 3) understand behavior and group dynamics of collared peccaries, and 4) describe population estimates over space and time for collared and white-lipped peccaries. We will explore these themes by asking the following questions: What are the detection rates of peccaries and what do they inform us about population trends? How do survey methodologies affect peccary detection rates? What environmental factors affect the detection rate of peccaries? How do habitat type, time of day, and distance from the lab clearing affect peccary group dynamics and behavior? How are peccaries distributed across the landscape? What are current population estimates? What were the historical abundances of collared and white-lipped peccaries?

Materials and Methods

Study area and data collection—We conducted mammal surveys at Estación Biológica La Selva in the Caribbean lowlands of northeastern Costa Rica (10˚26′ N, 83˚59′ W). La Selva, which is connected to Parque Nacional Braulio Carrillo (~480 km^2), is composed of primary forest, selectively logged primary forest, successional secondary forests, and abandoned pastures and plantations, totaling just over 16 km^2 (McDade and Hartshorn 1994). Annual average rainfall is ~4 m, with precipitation peaks occurring in June–August and October–November (Clark and Clark 2010, McClearn et al. in press). La Selva is a well-protected site with professional park guards patrolling the property. Still, guards find evidence of illegal hunting and encounter hunters on occasion. The mammalian fauna of La Selva is typical of Neotropical rainforests and the majority of species are of widespread distribution (Timm 1994).

We walked 5 pre-existing trails, on 348 survey days between September 2005 and June 2007, traversing primary forest, different types of secondary forest, managed successional areas, the arboretum, and the ecological reserve (Fig. 2.1). We walked 4 trails (1–4) diurnally and 1 trail (5) nocturnally, starting at ~0700 hr and 1900 hr, respectively. In the event of heavy rainfall during a survey, the observer paused until conditions improved, or abandoned the survey if it could not be completed by 1100 hr or 2300 hr. We employed powerful flashlights during night surveys to detect and identify animals. Throughout the survey, some trails occasionally were walked in the opposite direction. Trails were not of equal length, but we walked a total of 1,052.36 km (848.36 km diurnally and 204 km nocturnally), totaling 981.7 hrs.

During our survey, we walked at ~1 km/hr searching for collared peccaries and other mammals, and recorded the following variables: time of sighting, location of sighting, perpendicular distance from first observed animal to the trail, number of individuals, radius of group, and whether the animal was first detected by sight or hearing. We recorded peccary groups as 1 encounter. All distances were visually estimated. Only 1 observer walked the trails, except during the last 5 months of the survey, when 2 observers walked the diurnal portions of the survey together.

During analysis, we estimated the perpendicular distance from the trail such that animals within that distance were certain to be observed (the detection rate started to drop at that distance).

Detection rates—Detection rates were calculated in 2 manners: the number of encounters per hr walked (DRHr) and the number of encounters per km walked (DRKm). The 2 rates (DRHr and DRKm) were correlated to test if they were interchangeable. We used a Chi-square test, with expected values standardized by km walked diurnally and nocturnally, to test for activity differences during day and nighttime. We use diurnal data throughout this study, unless specified, because peccaries are not as active nocturnally.

To test for biases in detection rate due to increased sampling effort during the last 5 months of the survey, we used ANCOVA, because rainfall in this seasonal environment was found to be marginally significant. We omitted data from January 2007 because in this month the number of observers increased to 2.

The observer recorded if detection was based on sight (visual detection) or sound (vocalizations, or noises created by movement in the environment). To determine if peccaries were detected more by sight or sound, we performed a Chi-square goodness of fit test.

We plotted monthly DRKm through time to observe population trends. Because DRKm varied widely through time, we explored the amount of sampling effort needed to find a stable DRKm estimate. We randomized the order of the daily data (number of peccary sightings and kms walked) over 100 iterations and calculated a cumulative daily DRKm. We then found the amount of effort such that 95% of the cumulative daily DRKm stabilized within ± 10 % and ± 5% of the total DRKm.

Although our data initially appear to be suited for distance sampling (Buckland et al. 2001), several assumptions of the procedures are not met, rendering this method unsuitable. First, the ‘shape criterion,’ wherein the detection function should have a shoulder, implying that “detectability is certain near the line or point and stays certain or nearly certain for some distance” (Buckland et al. 2001), was not observed in our data. A histogram of perpendicular sighting distances shows a high proportion of sightings within 1 m from the trail, and a drastic reduction thereafter. Second, a spike in sightings closer to the trail, and differences in the perpendicular sighting distances in different forest types, suggest that peccaries are not uniformly distributed with respect to perpendicular distance from the line. Finally, the strong effect of the lab clearing on detection rates indicates that peccaries are not distributed in the area according to some stochastic process. Our peccary data highlight several pitfalls that may be associated with line transect sampling, particularly in meeting the assumptions of the tests.

Environmental factors—To test whether mean daily rainfall (mm), air temperature (°C), minimum air temperature (°C), and maximum air temperature (°C) of the current and/or previous month were associated with monthly DRHr, we performed a stepwise linear regression with alpha-to-enter and alpha-to-remove equal to 0.15. We calculated the values for these environmental factors from the Organization for Tropical Studies’ (OTS) meteorological weather stations at La Selva (http://www.ots.ac.cr/meteoro/default.php?pestacion=2).

Primary and secondary forest effects—We categorized each peccary sighting by forest type (primary versus secondary) by using GIS land use layers from the OTS La Selva Geographic Information Systems website (http://ots.ac.cr/index.php?option=com_wrapper&Itemid=352). Primary forest included primary forest and ecological reserves, and secondary forest included all secondary forest types.

We used a Chi-square test, with expected values standardized by km walked in each forest type, to assess preference for primary or secondary forest. We tested if group size, group radius, and perpendicular sighting distance from the trail were different in primary versus secondary forest. Group sizes, group radii, and sighting distances are not normally distributed; consequently, we used Mann–Whitney U tests. We used a contingency table and a Chi-square test with Yate's correction to test if the proportion of singletons in primary and secondary forest differed.

Diurnal and nocturnal differences—We tested whether group size, group radius, and perpendicular sighting distance are different for peccaries sighted diurnally and nocturnally by using Mann–Whitney U tests.

Effect of lab clearing—To determine whether distance from lab clearing (developed area that includes laboratory buildings and housing) affected peccary sightings, for groups and total number of individuals seen, data were entered into a geospatial framework using ArcMap 10. We created incremental rings of 300 m around the edge of the lab clearing and found detection rates (group DRKm and total number of individuals DRKm) for each transect within each ring. We regressed detection rates onto the distance from lab clearing using the middle distance of each ring as the value for the dependent variable (i.e., 150 m was used for the value of the 0–300 m ring). We compared regression models using SigmaPlot 9.0. Models were evaluated using R-squared, adjusted R-squared, Durbin–Watson statistic, and residual analyses. To assess the level of human foot traffic, we calculated a DRKm for the total number of people seen within each ring.

Correlations were done to test if group size was associated with distance from lab clearing, both including and excluding singletons. To test if the proportion of singletons was correlated with distance from the lab clearing, we created 11 bins, of 300-m increments, and correlated the bin distances with the calculated proportions of singletons within the bins. Pearson's correlation was used to determine if perpendicular sighting distance from trail was affected by distance from lab clearing. Distance from lab clearing for each encounter was calculated using ArcMap 10.

Spatial distribution—To assess changes in foraging areas through time, we delineated aggregations of peccaries based on natural clusters of group sightings over time for trails 1 and 3, the trails with sufficient data. We divided each trail into 300-m segments and calculated the percentage of times we walked the segment that included at least 1 peccary sighting. We also calculated an Index of Dispersion (variance/mean) for groups to determine how peccaries are dispersed in La Selva. We used 300-m segments as our sampling unit.

Population estimates—The population of peccaries in La Selva was estimated by censusing a 12.5 m strip on each side of the trail; 12.5 m was chosen *a posteriori* given that beyond 12.5 m the detectability of peccaries dropped considerably and was consistently low. Each survey day was then considered a replicate and estimates were calculated using the following formula: $\hat{D}_i = \frac{\bar{y}_i}{L_i \times .025}$, where $\hat{D}_i$ is the number of groups per km^2, $\bar{y}_i$ is the average number of groups seen each survey day for trail *i*, L_i is the total survey distance (in km), and 0.025 is the width of forest censused in km. Numbers of individuals for each trail were then estimated by $\hat{d}_i = \hat{D}_i \times \bar{g}_i$, where $\bar{g}_i$ denotes average group size. Mean group size was calculated for each trail independently to keep the scale of estimates the same. Assuming the 2 estimates $\left(\hat{D}_i, \bar{g}_i\right)$ to be independent of one another, $se\left(\hat{d}_i\right) = \sqrt{\hat{D}_i^2 s_{\bar{g}_i}^2 + \bar{g}_i^2 s_{D_i}^2 - s_{\bar{g}_i}^2 s_{D_i}^2}$, where s_{D_i} and s_{g_i} denote the standard errors of $\hat{D}_i$ and $\bar{g}_i$, respectively (Goodman 1960). We did not estimate densities for the entire station, but rather kept densities specific to each trail, because of the many arbitrary decisions involved (e.g., for what area of La Selva is trail *i* representative, especially in light of the effect of distance from lab clearing?).

Historical perspective—To assess changes in abundance over time of both collared and white-lipped peccaries, we reviewed pertinent published sources for Costa Rica's Caribbean lowlands and obtained unpublished historical data from a variety of sources. These unpublished sources include a 1979–86 logbook, where researchers at La Selva recorded mammal sightings. We used unpublished data collected by Devon Graham who from June 1991 to March 1992 recorded mammal observations, their location, group size, time of day, and behavioral notes. We also used unpublished data from Bruce E. Young, who was at the time the full-time director of La Selva, and Anya Illes who recorded mammal sightings intermittently between 1994 and 1997. To assess the state of peccary populations in the 1990's we calculated the percentage of mammal sightings that were peccaries, average group size, and largest group. We only included observations of mammals before 1900 h due to the behavior of peccaries and the focus of this study on diurnal sightings. To evaluate historical peccary populations further, we queried knowledgeable local residents and scientists who have vast experience working in Costa Rica's Caribbean lowlands during different time periods; this included an individual who hunted regularly in the area in the 1950s and 60s. We used Minitab v. 15 for all statistical tests, unless otherwise noted, and ArcMap 10 for all GIS analyses.

Results

We sighted collared peccaries 231 times (217 diurnal and 14 nocturnal); no white-lipped peccaries were observed. Group size ranged from 1–19, with averages of 3.94 (*SD* = 3.74, median = 2), and 5.48 (*SD* = 3.79, median = 4) with singletons included or excluded, respectively. Singletons made up 34.4% of sightings. Mean group radius was 7.7 m (*SD* = 9.00 m) with a range of 0.25–50 m. Animals that were on the trail or within 1 m of the trail represented 47.6% of sightings. The detection rate within 12.5 m from the trail stayed relatively constant, and then dropped, suggesting a significant proportion of groups beyond this distance might have been missed. Collared peccaries were the most frequently encountered mammal during the survey, comprising 27.3% of sightings.

Detection rates—DRHr for collared peccaries for diurnal and nocturnal surveys combined is 0.237, with a diurnal DRHr of 0.272 and a much lower nocturnal DRHr of 0.079. DRKm for diurnal and nocturnal combined, diurnal alone, and nocturnal alone are 0.220, 0.256, and 0.069, respectively. Peccaries were detected more often diurnally than nocturnally ($\chi^2_1 = 26.282$, $P = 0.0001$). The correlation between DRHr and DRKm is highly significant ($r = 0.973$, $P < 0.001$). Observer number did not significantly affect detection rates for peccaries ($F_{1, 16}$ for observer size = 0.03, $P = 0.871$). However, rainfall did have a marginal effect, with fewer sightings in rainy periods (see next section). A goodness of fit test showed that peccaries were detected significantly more often by sight than by sound ($\chi^2_1 = 22.59$, $P < 0.001$).

Monthly DRKm varied considerably with a high of 0.421 in April 2006 and a low of 0.068 in December 2005 (Fig. 2.2). There were no significant trends through time ($r = -0.045$, $P = 0.851$). The first 3 sampling months' DRKm were quite different from one another, including the lowest and second highest values. This had a large effect on the mean DRKm. Using the randomization procedure, we found that 95% of iterations stabilized within ± 10% of the total DRKm at 584.38 km (194 survey days), and within ± 5% at 778.98 km (257 survey days).

Environmental factors—The stepwise linear regression showed that among the variables: mean daily rainfall (mm), mean temperature (°C), maximum temperature (°C), and minimum temperature (°C) from the current and previous month, the only measured environmental factor associated with detection rates was rainfall, albeit only marginally significant ($R^2 = 0.188$, $P = 0.056$). This produced the relationship: detection rate = 0.348 – 0.00721 × mean daily rainfall (mm).

Primary and secondary forest effects—No preference was detected between primary and secondary forest ($\chi^2_1 = 0.006$, $P = 0.940$). Group sizes in primary forest (mean = 3.85, *SD* = 3.23, median = 3) and secondary forest (mean = 3.65, *SD* = 3.93, median = 2) were not significantly different ($U_{113, 86} = 11952.5$, $P = 0.096$). Group radius was larger in primary forest (mean = 9.30 m, *SD* = 10.08 m, median = 6 m) than in secondary forest (mean = 5.82 m, *SD* = 7.83 m, median = 3 m) ($U_{79, 47} = 5523.5$, $P = 0.010$). The proportion of singletons in primary forest (29.2%) was significantly smaller ($\chi^2_1 = 4.16$, $P = 0.041$) than in secondary forest (44.2%). Perpendicular sighting distance to trail was significantly greater ($U_{113, 85} = 12642$, $P = 0.0003$) in primary forest (mean = 4.42 m, *SD* = 5.03 m, median = 4 m) than in secondary forest (mean = 3.47 m, *SD* = 11.2 m, median = 0.25 m). The proportion of sightings on and within 1 m of the trail was 36.3% for primary forest and 62.4% for secondary forest.

Diurnal and nocturnal differences—For diurnal sightings, mean group size was 3.94 (*SD* = 3.72, median = 3), with 35% of the observations as singletons, whereas for nocturnal sightings the mean was 3.92 (*SD* = 4.13, median = 2), with 21.4% of observations as singletons. Group size was not significantly different between peccary groups sighted diurnally or nocturnally ($U_{215, 13} = 24997$, $P = 0.092$). Group radius was not significantly different ($U_{138, 9} = 10376.5$, $P = 0.183$) between diurnal sightings (mean = 7.84 m, *SD* = 9.15 m, median = 5 m) and nocturnal sightings (mean = 5.03 m, *SD* = 6.08 m, median = 3 m). The mean sighting distance from the trail was 4.03 m (*SD* = 8.22 m, median = 2 m) diurnally, and 2.96 m (*SD* = 3.21 m, median = 2.5 m) nocturnally and not significantly different ($U_{216,13} = 1487.5$, $P = 0.975$). The percentages of sightings within 1 m from the trail were 38.5% and 47.9% nocturnally and diurnally, respectively.

Effect of lab clearing—We evaluated a variety of regression models to determine the effect of distance from lab clearing on number of peccary groups and total peccary numbers. Based on R^2, Durbin–Watson statistic, and plots of the residuals of various models, it was clear that the relationship between peccary variables and distance from lab clearing (DLC) was best expressed by a curvilinear relationship, particularly a single, 2 parameter exponential decay function. The best fit equation for number of peccary groups is: DRKm = 0.5603 $e^{(-0.0006*\mathrm{DLC})}$ (R^2 = 0.5785 and P = 0.0004, n = 17) (Fig. 2.3). The best fit equation for total number of peccaries is DRKm = 2.2157 $e^{(0.0005*\mathrm{DLC})}$ (R^2= 0.4442, P = 0.004, n = 17) (Fig. 2.3). In other words, the number of peccary groups and the number of total peccary individuals is higher near the lab clearing. DRKm for foot traffic was typically higher closer to the lab clearing, especially at 300–600 m (Fig. 2.3).

Group size was not significantly correlated with DLC, regardless of whether singletons were included (r = 0.093, P = 0.175, n = 215) or excluded (r = 0.086, P = 0.312, n = 140) in the analysis. Moreover, the proportion of singletons, in 300 m bins, was not significantly correlated with DLC (r = -0.372, P = 0.259, n = 11). Perpendicular sighting distance from the trail was not correlated with DLC (r = 0.058, P = 0.399, n = 217).

Spatial distribution—Due to the different number of times each trail was walked, spatial analyses were completed separately for each trail. On trail 1, peccaries appear to be relatively regularly distributed. However, when distributions are plotted by year, it becomes obvious that peccary groups are clumped in several areas. To elucidate this pattern further, it can be observed from Fig. 2.4 that on several 300 m segments of the trail (segment 3, 6–9) peccaries were rarely seen compared to segments 1–2 and 4–5. On trail 3, this pattern is repeated in that segments vary widely in the probability of a peccary encounter (Fig. 2.4). To support these findings, the Dispersion Index (s^2/x̄) for groups in trails 1 and 3 are extremely high (4.83, 3.98, respectively). These high values suggest a clumped distribution. However, on trails 2 and 4 the Dispersion Index for groups (1.6, 1.1, respectively) suggests a random distribution.

Population estimates—Estimated peccary group densities range from 3.7 on trail 2 to 20.7 groups/km^2 on trail 1 (Table 2.1). The density of individuals range from 19.1 on trail 4 to 65.9 peccaries/km^2 on trail 1 (Table 2.1).

Historical perspective—The La Selva logbook from 1979–1986 has a total of 1,009 mammal sightings, 75 of which are peccaries. Only 3 peccary sightings occurred in 1979, all of which were white-lipped peccaries. White-lipped peccary sightings at La Selva past 1979 cannot be confirmed, as observers were uncertain about which peccary species was seen.

Unpublished data from D. Graham cited a total of 271 diurnal mammal sightings. Mammal sightings were recorded for 154 days, and 67 of the total sightings were collared peccaries, 39 of which occurred in the lab clearing. Mean group size was 3.6 (*SD* = 3.6), and 4.9 (*SD* = 3.8) including and excluding singletons, respectively. The largest group size observed was 15–20 individuals, and 32.8% of his peccary sightings were singletons.

Unpublished mammal observations by B. E. Young and A. Iles collected during 103 days between 1994 and 1997 include 207 sightings, 47 of which were collared peccaries. Mean group size for this data set including and excluding singletons is 5.03 (*SD* = 6.09), and 7.25 (*SD* = 6.62). The largest group was 24 peccaries, and 23.4% of their sightings were singletons.

Historical information and comments gathered concerning white-lipped and collared peccaries at La Selva and elsewhere in the Caribbean lowlands are presented in Table 2.2, and represented graphically in Figure 2.5.

Discussion

Collared peccaries were the most frequently sighted mammal during this study. They are considered common at La Selva because peccary groups are seen daily around the lab clearing and on the neighboring trails. No white-lipped peccaries were observed during this survey, nor have any been observed at La Selva for > 35 years.

Group size—Mean group size for collared peccaries at La Selva is within the range of those reported in the literature (Table 2.3). Herds in the northern, and more arid, parts of the range are larger than in Central and South America. Factors potentially accounting for small group sizes in the tropics include hunting pressure, response to environmental conditions, distribution of food resources, or observer visibility (Green et al. 1984; Sowls 1997). We discount hunting pressure as a cause for small group size, even though poaching still occurs at La Selva and in the adjacent Parque Nacional Braulio Carrillo, because peccary abundances are relatively high (see below) and because our survey was not conducted at the periphery of the reserve, where poaching is more likely to occur. Understory growth at La Selva may account for reduced sightings at a critical distance from the trail, because vegetation can obscure part of a group. Torrealba and Rau (1994) estimated mean group size for several herds at La Selva, based on the number of individuals entering sleeping sites, and reported averages of 9–27, with an average size of diurnal subgroups of 3–5. Thus, the small group sizes seen here can reflect that peccary herds in the tropics may be rather fluid and may disband into smaller subgroups during the day.

Throughout the range of collared peccaries, singletons range from being infrequently seen to comprising up to 44% of all sightings (Table 2.3). At La Selva, 34.4% of sightings were singletons, which is higher than proportions reported in Texas and Venezuela, but lower than in Panama and Peru (Table 2.3). Differences in the number of singletons have been found in tropical deciduous and semideciduous forests (Mandujano 1999), and likely differ in response to environmental conditions and herd dynamics. Singletons were thought to be old males that had left the group (Leopold 1959), or disabled animals (Schweinsburg 1971), but Oldenburg et al. (1985) found solitary young and old peccaries that were healthy. Keuroghlian et al. (2004) found no evidence of subgrouping for prolonged periods of time in Brazil, but 1–3 individuals would often forage separately for several hours. It is unlikely that the high proportion of singletons seen at La Selva represents old males or disabled animals, but rather evidence that herd stability and cohesiveness differs across the tropics. The high occurrence of subgroups and singletons may be due to environmental factors as small groups remained common throughout all seasons of our study, and in arid regions, subgroups and singletons occur in higher frequencies following periods of precipitation and when vegetation appears to be most dense (Oldenburg et al. 1985).

The physical spread of a peccary group has rarely been quantified or addressed in the literature. Variability in mean group radius is probably due to environmental conditions, group size, interactions among herd members, foraging, and threat of predation. In Texas, 94% of singletons and subgroups have a separation distance from the main group of 100–599 m, though it may be as far as 1,400 m (Oldenburg et al. 1985). Unfortunately, no data are available to compare the spread of individuals in their functional subgroups to our mean spread of 7.7 m.

The large proportion of sightings close to the trail (47.6% within 1 m) could be a consequence of difficulty in sighting peccaries through the dense understory, or more likely because peccaries prefer to move or aggregate on more open trails (for example, for ease of movement, foraging resources, and/or heightened predator detection). The dense understory may account for reduced visibility at a critical distance from the trail; however, it is unlikely that detectability greatly declines 1 m from the trail. Peccaries can be noisy as they forage and move, are fairly large animals, and can be detected by smell. The estimated distance from the trail beyond which a significant proportion of peccaries were missed was 12.5 m, and although shorter distances likely have higher detection probabilities, the difference in detection is small within the 25 m strip. Therefore, the large proportion of peccaries close to trails almost certainly represents a behavioral preference.

Detection rates—The survey was walked at ~1km/hr and, therefore, DRHr and DRKm are very similar. We use DRHr and DRKm interchangeably, depending on which rate was appropriate for the analysis (e.g., DRKm was used for spatial analyses). The switch from 1 to 2 observers during the last 5 months of the survey did not affect DRHr, so we did not adjust the data for increased sampling effort. We recommend that when surveying collared peccaries, if 2 observers are available, it is better to have observers walk different transects simultaneously to maximize data collection. Collared peccaries can be loud and are easy to hear when threatened. However, during our survey we detected more peccaries visually than by sound. These findings give us confidence that we usually detected peccaries before they detected us and modified their behavior or position.

DRHr and DRKm for diurnal surveys are much higher than for nocturnal surveys (14 of 231 sightings were nocturnal), and thus collared peccaries should be sampled diurnally. We excluded the nocturnal data from most of our analyses. Monthly DRKm did not show any significant trends. Moreover, monthly DRKm were quite variable, especially in the first 3 months, which included the lowest and second highest DRHr. Using the randomization procedure, our data show that rapid surveys may be useful to detect the presence of a species, but may result in inaccurate detection rate estimates.

Environmental factors—The only environmental factor that marginally affected DRHr was mean monthly rainfall. Rainfall can affect fruit availability in the Neotropics (Keuroghlian and Eaton 2008), and in turn influence DRHr by altering peccary behavior and foraging strategies. Although collared peccaries may modify their diet during times of fruit scarcity (Bodmer 1990), the effects of seasonality and rainfall have been linked to changes in feeding pattern dispersion (Bigler 1974), home range size, and level of activity and movement (Judas and Henry 1999; McCoy and Vaughan 1990). DRHr variation because of rainfall strongly suggests that care should be taken when comparing sites, or the same site, if surveys were conducted during different seasons. Surveys were never started during heavy rainfall, and in the event of rainfall during a walk, observers paused until conditions improved. Therefore, DRHr was not affected by visual obstruction due to rain, and was likely a result of some behavioral modification, though we do not have data to explore this further.

Primary and secondary forest effects—Peccaries do not exhibit habitat preference between primary and secondary forest at La Selva, which is consistent with previous studies (Reyna-Hurtado and Tanner 2005; Sowls 1997; Tobler et al. 2009). Collared peccaries do show a preference for areas with canopy cover (Green et al. 2001), and an aversion to farmlands (Tejeda-Cruz et al. 2009). Hunting pressure also has an effect on habitat choice (Reyna-Hurtado and Tanner 2005).

Group size was not different in primary and secondary forest. However, the proportion of singletons in secondary forest is higher than in primary forest. Group radius and sighting distance were higher in primary forest. If secondary forest undergrowth makes peccary detectability harder, we might predict the greater sighting distance in primary forest and a higher proportion of singletons in secondary forest (some individuals in a small group are missed). However, recall that about half of the peccary sightings are within 1 m of the trail and many more sightings are within 3 m of the trail, so dense understory in secondary forest would not influence detectability. The decreased group radius in secondary forest could indicate higher vigilance in areas of limited visibility or different dispersion of food sources.

The decreased perpendicular sighting distance from the trail in secondary forest was statistically different, but may not be biologically significant. The difference in means was 1 m, and the difference of the medians, which were the values statistically tested, was 3.75 m. Given the spatial scale in which peccaries move and forage daily, ±3.75 m from the trail may or may not be a signal of differential use of the open trails in primary and secondary forest. If this difference is biologically significant, it suggests that peccaries prefer to forage or move in more open areas closer to the trail in secondary forest, perhaps indicating differences in predator–prey interactions in these different forest types. Little is known about the distribution of peccaries and their predators through time and space, and prey-seeking and predator-avoidance/fleeing behaviors, though Weckel et al. (2006a) showed jaguars prefer trails. At La Selva, the large predators of collared peccaries include the puma and jaguar. Jaguars have not been seen at La Selva for several years, though camera traps have captured this species along the Braulio Carrillo altitudinal transect connected to La Selva, and individuals likely reside or roam within the station, at least on occasion. Pumas are much more common, with visual sightings and confirmation via camera traps.

Effect of lab clearing—Distance from lab clearing did not affect group dynamics of collared peccaries, but did have a strong effect on the number of groups and the total number detected, with more observed near buildings. Groups and total number of peccaries exponentially decayed within 1 km and stabilized thereafter.

A higher number of peccaries seen closer to the lab clearing may be due to several factors that contribute to their true presence and detectability. First, peccaries may be more easily observed near the lab clearing because they are habituated to human activity, and there are greater and reliable food resources. Collared peccaries habituate readily, as reported for "urban" and "non-urban" peccaries in Arizona (Bellantoni and Krausman 1993). Individuals closer to the lab clearing are observed daily, sleep under buildings, and are less wary of observers than those at the back of the property. Peccaries closer to the clearing have repeated contact with humans and allow people to approach them, or they themselves approach people. Similar habituation was observed at La Selva in the 1990's, when peccary sightings in the clearing became common. Preference to gather in lab clearings has been observed on Barro Colorado Island for coatis (*Nasua narica*), and is presumably due to the plentiful availability and handouts of food (Kaufmann 1962, McClearn 1992). At La Selva, biologist M. Knörnschild had several encounters of peccaries crossing behind her on a ~1.5 m wide, ~100 m long bridge (Table 2.2). Romero (pers. obs.) observed a visitor holding bread fruit (*Artocarpus altilis*; Moraceae) in the lab clearing while a peccary ate it. In contrast, peccary groups in the back of the property are nervous and when detecting an observer would growl, woof, clack their teeth, and run away quickly, but this behavior increases detectability. In addition, the perpendicular sighting distance was not correlated with distance from lab clearing, making it improbable that we overlooked peccaries in the back of the property. Thus, the higher number of sightings closer to the lab clearing represent their true presence and not behavioral differences nor visibility.

Second, there may be more peccaries closer to the lab because high foot traffic of researchers and tourists could keep predators away. More large feline (puma or jaguar) scat and tracks (including sets of an adult with a juvenile) were seen farther back in the property, although at least 1 puma occasionally hunts within ~300 m of the lab clearing. Smaller feline scat (probably ocelot) was seen throughout La Selva (Romero, pers. obs.). All large cat scat found contained peccary hair.

Third, collared peccaries probably are one of the most frequently hunted mammals within La Selva, and hunting likely takes place farther away from the lab clearing as it is easier to enter the forest and hide from guards, researchers, and tourists. Although La Selva is one of the best protected areas in the tropics with trained park guards routinely patrolling, poaching still occurs. Hunters, hunting dogs, and evidence of hunting (butchered animals) are occasionally seen.

Finally, there may be environmental factors, such as the proximity to floodplains, that influence the abundance of peccaries. Collared peccaries can respond to habitat and resource differences at small scales (~1 km^2) (Fragoso 1999). The lab clearing is at the confluence of 2 rivers, and flooding, with several meters of water, occurs yearly. Flood patterns affect this area ecologically, with flood plain soils being the most productive soils of the reserve, perhaps making it more desirable for peccaries. However, floodplains are in close proximity to other surveyed trails (e.g., trail 4), which are far away from the lab clearing and do not have an abundance of peccaries.

Diurnal and nocturnal behavior—It is obvious from DRHr that collared peccaries in the Caribbean lowlands of Costa Rica are diurnal/crepuscular animals. Although some authors suggest that this species is active during the night (Ellisor and Harwell 1969), our study shows that very few peccaries were encountered after dusk. Of the 14 nocturnal observations, several were of sleeping groups that were startled when approached. The sleeping groups were typically large and took advantage of manmade structures, for example, underneath stilted buildings in the forest or in the lab clearing. Other nocturnal observations occurred at the beginning of a survey and were of groups that were feeding, likely before retreating to sleep. We acknowledge that comparing data on group dynamics of 217 diurnal observations to 14 nocturnal sightings is not a balanced or robust design, but nonetheless we believe that this information can be used as a building block to understand peccary behavior after dusk.

Group size (median and mean) is not different for diurnal and nocturnal observations. Due to our small sample size of nocturnal observations, we could not statistically test if the proportion of singletons differed; however, our data suggest fewer singletons are observed at nighttime (21.4% vs. 35%). This difference could be attributed to the survey technique itself (harder to see a singleton in the dark), or more likely, because fluid groups disband into smaller subgroups during the day and fuse back together at night. Neither group radius nor perpendicular sighting distance differs for diurnal and nocturnal observations, although the proportion of sightings within 1 m of the trail was 9% higher nocturnally. This suggests that peccary groups may not be increasing their vigilance by decreasing the spread of the group, nor changing their behavior to cluster on more open trails nocturnally. Given that our perpendicular sighting distance was not significantly different diurnally or nocturnally, we believe that the fewer observations of peccaries at nighttime are due to fewer peccaries being active, rather than difficulty in spotting them. Little information is available about the nighttime behavior of peccaries, and understanding nocturnal behavior will be important to decipher further diurnal group dynamics.

Spatial distribution—A map of sightings over the course of the entire survey shows peccaries on all parts of the trails. However, for trails 1 and 3, separation of data by year reveals distinct areas where peccaries are frequently observed. These areas are relatively consistent year to year, though some shifts did occur. The results of the Dispersion Index reinforce these map observations, showing that peccary groups are clumped for trails 1 and 3. The random distribution for trails 2 and 4 may be a statistical artifact of low encounter rates. For this reason we graph only the probability of encounter for trails 1 and 3 (Fig. 2.4).

As we conducted our surveys on trails 1 and 3, the clumped patterns could have been because: 1) we were detecting several subgroups within the larger herd's home range, 2) different groups frequent the same spot with agreeable habitat characteristics such as food or shelter, and/or 3) we repeatedly encountered the same group in the same spot. For trails 2 and 4, the spatial distribution question is trickier to answer due to the lower number of sightings, though there also are areas of higher use. The spatial distribution patterns shown by our study may be more representative of the arrangement of subgroups, given the mean group size observed. However, our sampling methods do not allow us to determine how and why herds are distributed across the landscape.

Population estimates—Estimating peccary densities is a difficult task, and a full understanding of the data, field methods, and statistical analysis is essential. We could not assign a density estimate for La Selva due to the conspicuous relationship between peccary detection rates and distance from lab clearing. Rather, we estimated densities for each diurnal trail separately. Attempting to extrapolate densities for the whole station is problematic because there are too many arbitrary decisions to make (e.g., for what area of La Selva is trail *i* representative?). We, therefore, present peccary density estimates for groups (likely subgroups) and individuals for each trail. We believe that these trail density estimates will be useful data on the state of peccary populations in La Selva today and provide baseline information against which future surveys can be compared for the purpose of establishing directionality and intensity of any trends.

Peccary densities at La Selva were estimated to be 19.05, 21.05, 38.72, and 65.92 individuals/km^2 for trails 4, 2, 3, and 1, respectively (Table 2.1). Although these estimates vary greatly within La Selva, they should not be taken as the lower and upper limits of densities for the entire property. For example, the density on trail 1 is much higher than for other trails. Yet, trail 1 is likely only representative of areas in La Selva which are close (~1 km) to the lab clearing, a relatively small area due to its proximity to the natural boundaries of the rivers. In contrast, trail 4, which traverses a large portion of the back area of the property, would likely be representative of a larger area. Therefore, it is inaccurate to combine these densities to calculate an average estimate for La Selva.

The estimate for trail 1 is higher than densities reported elsewhere in the Neotropics (Table 2.4). Estimates for trails 2–4 are also high, but within the range of densities found on Barro Colorado Island. These high estimates could be due to a number of factors. For example, both La Selva and Barro Colorado Island are some of the best protected field stations in the Neotropics, and hunting pressure is likely low. Additionally, La Selva has high net primary productivity (NPP), even higher than some areas in the Amazon, and thus may support higher abundances (D. B. Clark, pers. comm.).

Although density estimates provide informative data, caution should be exercised when comparing estimates from other sites and/or different time periods. Densities of peccaries can fluctuate quickly, e.g., a ~65% change in 4 months on Barro Colorado Island (Wright et al. 1999). Consequently, surveys done to compare densities at different sites should be done in a manner to account for population trends and fluctuations. Additionally, estimates calculated via different field and/or statistical techniques should not be directly compared. For this reason, we cannot compare Torrealba and Rau's (1994) density estimate of 14±1 individuals/km^2 to our current estimates and assign a change or directionality to peccary populations. Peccary populations in the Caribbean lowlands of Costa Rica likely exhibit natural fluctuations through time. To understand larger scale population changes, and the potential ecological impacts these changes have in the ecosystem, a thorough understanding of these populations in a current and historical perspective is imperative.

Historical perspective—Published historical peccary densities for Costa Rica's Caribbean lowlands are limited. However, inferences on the populations of peccaries through time can be made from travel notes, published scientific accounts, and observations from individuals familiar with the area.

Early accounts of the Caribbean lowlands indicate that white-lipped peccaries were abundant, found in large herds, and regularly hunted. Samuel A. Bard (a pseudonym for Ephraim G. Squier) (1855:281–224) depicted white-lipped peccaries along Nicaragua's Caribbean coast as common, and described their "ravenous" feeding, which included snakes and reptiles (Table 2.2). Thomas Belt, the British naturalist, also commented on white-lipped peccaries along the Costa Rica–Nicaraguan border from his travels up the Río San Juan, and mentions herds of "fifty to one hundred" in the lowlands (Belt, Table 2.2). Alston (1879–1882:110) described white-lipped peccaries in the Costa Rican lowlands as "found in great droves" and somewhat common at higher elevations (Table 2.2). These brief accounts indicate that in the 19th century white-lipped peccaries were abundant and found in large herds in the Caribbean lowlands.

White-lipped peccaries in the lowlands surrounding La Selva could be found in herds of over 100 individuals in the 1930–40's, even though they were heavily hunted. Evidence of large herds was apparent by how they affected the forest floor (Alvarado-Díaz, Table 2.2). The first written account of peccaries at La Selva is from Slud (1960) in 1950's (Table 2.2). He comments on white-lipped peccaries but makes no mention of collared peccaries, which is a complete reversal of the peccary situation today. Around the 1950's, white-lipped peccary populations were decreasing in the Caribbean lowlands, although large populations still persisted (Alvarado-Díaz, Table 2.2).

Historically, white-lipped peccaries were the most common of the 2 species at La Selva, being abundant in the lowlands and at higher elevations on Volcán Barva at El Plástico–Rara Avis (500–700 m). Through the early to mid-1960's, a La Selva staff member considered them a nuisance and their effect on the leaf litter was apparent (Janzen; Bien, Table 2.2). Large herds were hunted, and by the late 1960's white-lipped peccaries were disappearing (Janzen; Bien; Alvarado-Díaz, Table 2.2). The last herd of white-lipped peccaries in the Río Bijagual area (at ca. 300 m) was shot in 1971 (Foster, Table 2.2).

In the 1970's, both white-lipped and collared peccaries were present in low densities at La Selva, and likely throughout the altitudinal transect to Braulio Carrillo. Through the 1970's, evidence of white-lipped or collared peccaries was limited to few observations of individuals or tracks. At La Selva, a herd of > 20 white-lipped peccaries was seen by Rafael Chaverria (early 1970's), and a single individual was seen by LaVal (1973–74) (LaVal; Hartshorn, Table 2.2). The last reported sightings of white-lipped peccaries at La Selva are in the 1979 logbook, where 3 observations of small groups (~10, 6, and 3 individuals) were recorded (1 observation confirmed with original observer) (Beach, Table 2.2). Throughout the 1970's, herds of white-lipped peccaries must have been greatly reduced, and collared peccaries were rare, both likely caused by hunting pressure (Table 2.2).

In the early 1980's, no evidence of white-lipped peccaries was noted at La Selva and collared peccaries were still rare. By 1983, locals reported white-lipped peccaries to be rare or absent in the altitudinal corridor (Pringle et al. 1984). Hartshorn and Wilson never encountered white-lipped peccaries during their altitudinal transect work in the mid 1980's, although evidence of wallows believed to be from this species were seen, and few tracks of collared peccaries at El Plástico–Rara Avis were observed from 1983 to the early 1990's (Bien, Table 2.2). By the 1980's small groups, if any, of white-lipped peccaries (~15 individuals) inhabited the area, whereas collared peccaries were becoming abundant at La Selva (Alvarado-Díaz Table 2.2).

This is consistent with the 1979–86 logbooks at La Selva (Timm et al. 1989). It is difficult to assess the precise time of extirpation of white-lipped peccaries at La Selva because in the 1980's observers were uncertain of which peccary species were encountered. Nonetheless, these data provide information regarding peccary populations because in 1980, collared peccaries begin to appear regularly in the records, albeit in low numbers. Peccary populations, regardless of the species, must have been low from 1979–1986 because the proportion of peccary sightings to other mammal sightings during this time is low (0.01–0.14).

By the late 1980's, collared peccaries became more abundant at La Selva. Collared peccaries were commonly seen, and their growing group size and physical impact on the forest floor, such as the appearance of wallows was apparent (Clark, Table 2.2). Interestingly, a forest guard believed that collared peccaries were becoming a nuisance (Clark, Table 2.2). By the 1990's, collared peccary groups were conspicuous around the lab clearing (Graham, LaVal, Timm, and Young, unpublished data). We cannot use these data to calculate population densities or detection rates, but details are consistent with this study (mean group size, largest group, and percent singletons). The most quantitative historical data on collared peccaries at La Selva used radio-telemetry, documenting variability in group sizes and home ranges among different groups and months, and reporting a mean total annual home range of ~ 70 ha, and absolute density of 14

± 1 individual/km^2 (Torrealba and Rau 1994). The density and group dynamics, especially group size, of collard peccaries can be directly affected by competition with other species (Gabor and Hellgren 2000). Although not strong evidence, the similarity of group dynamics in these datasets possibly indicates that peccary abundances in La Selva throughout the 1990's and during this study were similar.

The last confirmed sighting of white-lipped peccaries in the La Selva–Braulio Carrillo complex was in 1993, when a pair was seen on the road to El Plástico (ca. 500 m). No white-lipped peccaries were seen at Rara Avis (in 2010), or at La Selva and higher elevation sites in Braulio Carrillo (2003–current) via camera-traps (Bien, Table 2.2, J. Hurtado, pers. comm.). At higher elevation sites, the abundance of collared peccaries may be increasing currently (Bien, Table 2.2). White-lipped peccaries have been extirpated from La Selva likely since the 1970's, and today are seemingly extirpated from the entire La Selva–Braulio Carrillo complex and have been since the 1990's. Small populations of white-lipped peccaries still persist in some remote areas of the Caribbean lowlands.

The extirpation of white-lipped peccaries, and decreased hunting pressure, may have allowed populations of collared peccaries to increase. Historical data to test whether the population density of collared peccaries has increased since the extirpation of white-lipped peccaries are not available, but all personal accounts and historical information support this hypothesis (Fig. 2.5). It appears that after the extirpation of white-lipped peccaries there was some lag time, but eventually white-lipped peccaries were replaced by collared peccaries. What remains a bigger challenge to discern is what ecological impacts, if any, occurred after the extirpation of white-lipped peccaries and the subsequent increase of collared peccaries.

Ecological impacts of shifting peccary populations—The ecological impacts of shifting peccary populations will be difficult to assess and only inferences can be made based on the ecology and behavior of peccaries in other habitats. White-lipped and collared peccaries differ in key ecological aspects, but may perform similar ecological functions. White-lipped peccaries are larger, and live in large, cohesive herds (Fragoso 1998; Sowls 1997). Group size is variable, and likely affected by hunting and habitat fragmentation, but often number in the hundreds. Anecdotal, historical reports describe herds of white-lipped peccaries of 300–2,000 individuals (Jardine 1836; Perry 1970; Sowls 1997). In contrast, collared peccaries live in smaller herds of 2–50 individuals, which are more fluid and often disband into subgroups (Sowls 1997). Collared peccary home ranges are smaller than those of white-lipped peccaries (Sowls 1997).

Despite the ecological and behavioral differences between the 2 peccary species, striking similarities exist on how these species interact with, and alter, their environment directly and indirectly. In terms of diet, white-lipped and collared peccaries have considerable overlap for species and items consumed (Barreto et al. 1997; Beck 2006; Desbiez et al. 2009; Kiltie 1981), though white-lipped peccaries have a stronger bite force that allows them to handle harder seeds (Beck 2006; Kilte 1982). White-lipped and collared peccaries affect plant density, composition, spatial distribution, and demography (Beck 2006; Fragoso 1997; Keuroghlian and Eaton 2009), likely in similar ways, with a particularly large effect on palms because palms make up over 60% of their diet (Beck 2006; Bodmer 1990; Kiltie 1981; Kiltie and Terborgh 1983). The reported overlap in palm species consumption for both peccary species is 59%, and they prey upon the same seed species at similar frequencies (Beck 2006).

Peccaries affect plant communities, especially the palms, via seed predation, seed dispersal, seedling trampling, herbivory, and foraging strategies, to the degree that they have been called ecosystem engineers (Keuroghlian and Eaton 2009, for review see Beck 2006). For example, peccaries are primarily seed predators (Kuprewicz 2013), but can also act as seed dispersers (Lazure et al. 2010). Peccaries account for high seedling and sapling mortality near parent trees, and the trampling and burying of seeds helps protect the seeds from predation by insects and increases germination rates, altogether affecting the spatial distribution of seedlings (Fragoso 1997; Silvius 2002). The magnitude of the impact peccaries have on their environments has been illustrated in several studies. For example, Wyatt and Silman (2004) showed an increase of uneaten palm seeds (5,340% for *Iriartea deltoidea* and 6,000% for *Astrocaryum murumuru*), and lowered seedling mortality when white-lipped peccaries are absent. Silman et al. (2003) documented that when white-lipped peccaries were absent during a 12-year period, the number of *Astrocaryum* seedlings increased by 70%, only to decrease by 71% after the recolonization of peccaries. In the early 1980's, Hartshorn wrote: "The most striking aspect of the La Selva forest is the richness and abundance of subcanopy, understory, and dwarf palms …" (Hartshorn 1983:136). Today however, the understory palms are not as abundant as in the early 1980's (Timm, pers. obs.). The effects that peccaries have on plants directly affect the plant community and must indirectly impact the community composition and diversity of other organisms.

White-lipped and collared peccaries also have important ecological impacts on the animal communities, although these have been studied less. Peccaries are ecosystem engineers because their wallows create higher ß diversity, species richness, and a higher density of tadpoles, metamorphs, and adult anurans than ponds (Beck et al. 2010). Areas with collared peccaries have higher encounters of reptiles and amphibians, and more juvenile anurans than peccary exclosures (Reider et al. 2013). Peccaries appear to prefer seeds that are infested with insect larvae, which may result in population control of certain insects (Fragoso 1994; Silvius 2002). In addition, they consume animals, including invertebrates, frogs, snakes, turtles, fish, eggs, eels, lizards, birds, and small rodents (Fragoso 1999; Gamero Idiaquez 1978; Husson 1978) in a manner that may significantly affect these populations (Carr; Table 2.2). Furthermore, the manner and extent to which peccaries transform their environment by altering the vegetation, leaf litter (Reider et al. 2013), and other aspects of the habitat probably, directly and indirectly, have cascading effects of other taxa.

It is hypothesized that white-lipped peccaries outcompete collared peccaries because of their larger herd size and aggressive temperament (Altrichter and Boaglio 2004; Mendes Pontes and Chivers 2007). Though the effects of white-lipped peccaries on collared peccaries have not been studied, niche overlap among white-lipped, collared peccaries, and feral pigs (*Sus scrofa*) is highest between the 2 peccary species (Desbiez et al. 2009). Collared peccary populations that are sympatric with feral pigs have 5–8 times lower densities, smaller group sizes, and larger territories (Gabor and Hellgren 2000). Therefore, it is likely that a species with a higher niche overlap than feral pigs, the white-lipped peccary, could affect collared peccaries in similar, if not more drastic manners. Studies elucidating the degree of competition between peccary species, and the resulting impacts on population parameters, are important for understanding historical and current forest changes. Even though we lack historical density information of white-lipped peccaries at La Selva, it is likely that substantial numbers of large herds ranged throughout the Caribbean lowlands (Janzen, Table 2.2), and were heavily hunted (Alvarado-Díaz, Table 2.2). Given our historical information about peccaries at La Selva, collared peccaries were seemingly at low densities when white-lipped peccaries were common, perhaps due to direct competition and/or hunting pressure, and that there was some lag time between the extirpation of white-lipped peccaries and the increase of collared peccary densities. White-lipped peccaries alter their environments in considerable ways (Keuroghlian and Eaton 2009; Silman et al. 2003; Wyatt and Silman 2004), so the transition period with no white-lipped peccaries and only small populations of collared peccaries probably produced a unique vegetation community at La Selva. Interestingly, this lag period corresponds to the rapid increase in research conducted at La Selva and to the concept of what constituted the “normal” La Selva forest. Although the 2 species differ, they share many traits that can result in collared peccaries having similar impacts on the environment today as white-lipped peccaries did historically. Thus, the current dominance of collared peccaries must not be considered as negative or abnormal without proper consideration and study of the relationship between peccary species, their impact on the environment, and a sound understanding of the area’s complex ecological history.

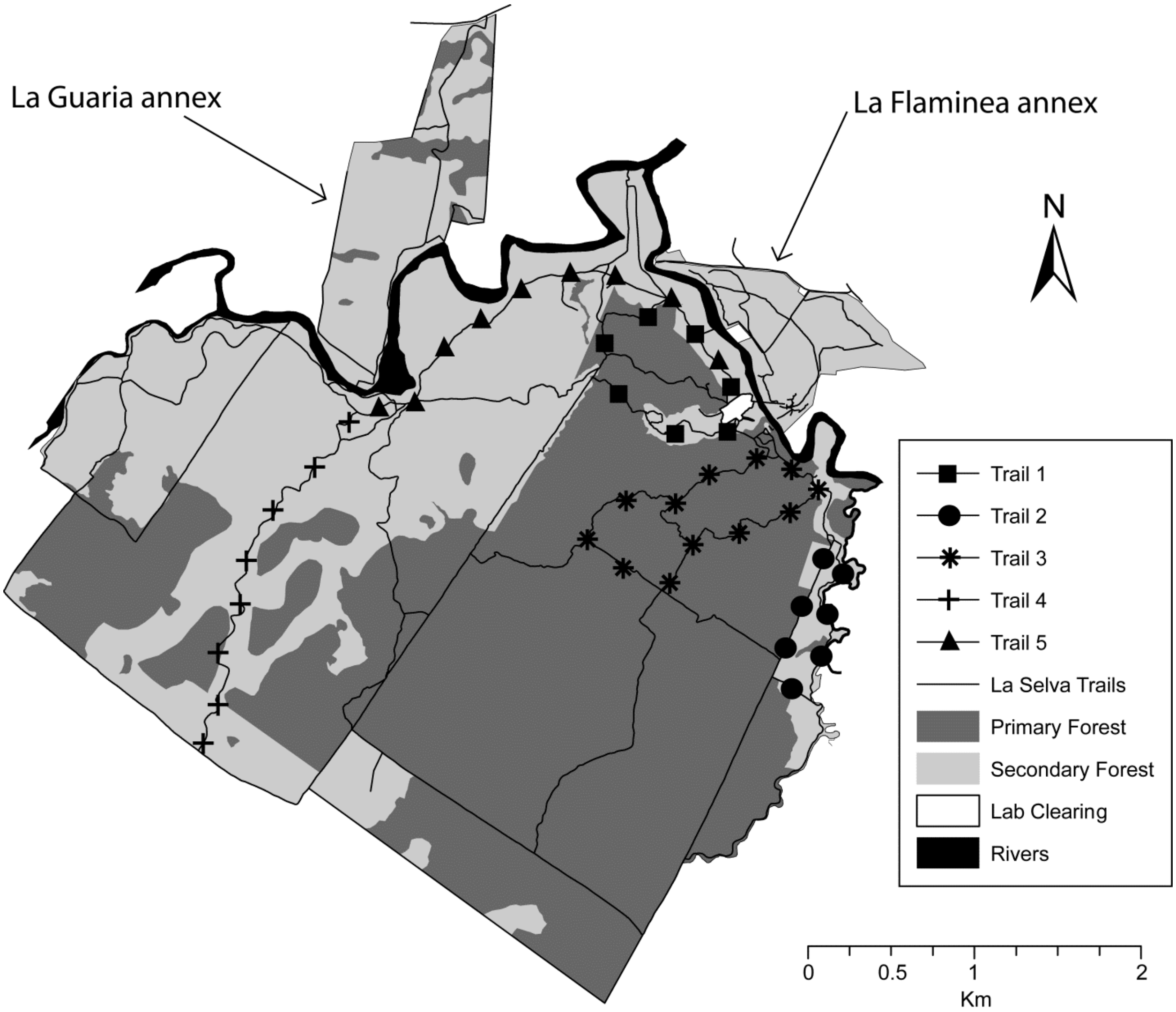

Figure 2.1—Map of La Selva Biological Station, in Sarapiquí, Costa Rica. Trails 1–4 were walked diurnally, and trail 5 nocturnally, for this study.

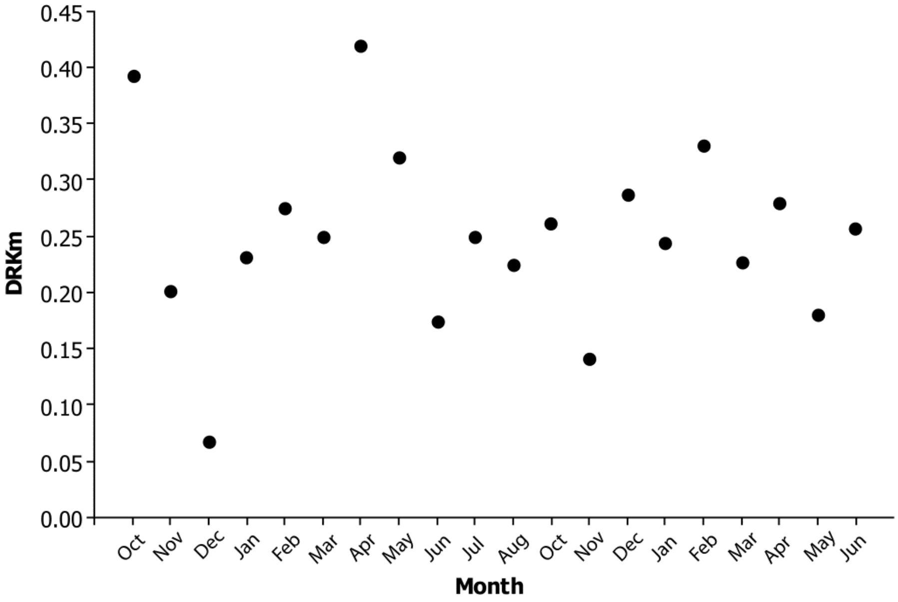

Figure 2.2—Monthly detection rates per km for all months surveyed.

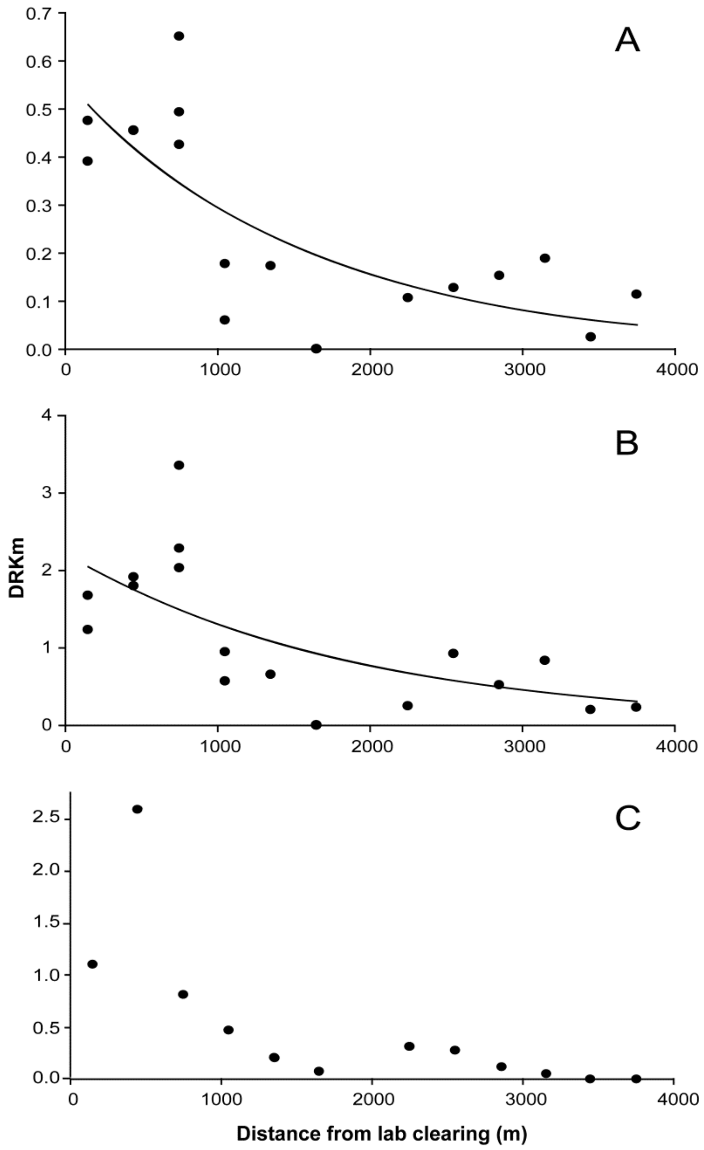

Figure 2.3—Detection rates by km for varying distances from the lab clearing for A) groups of peccaries for each trail, B) total number of peccaries observed for each trail, and C) number of people observed in each 300 m segment.

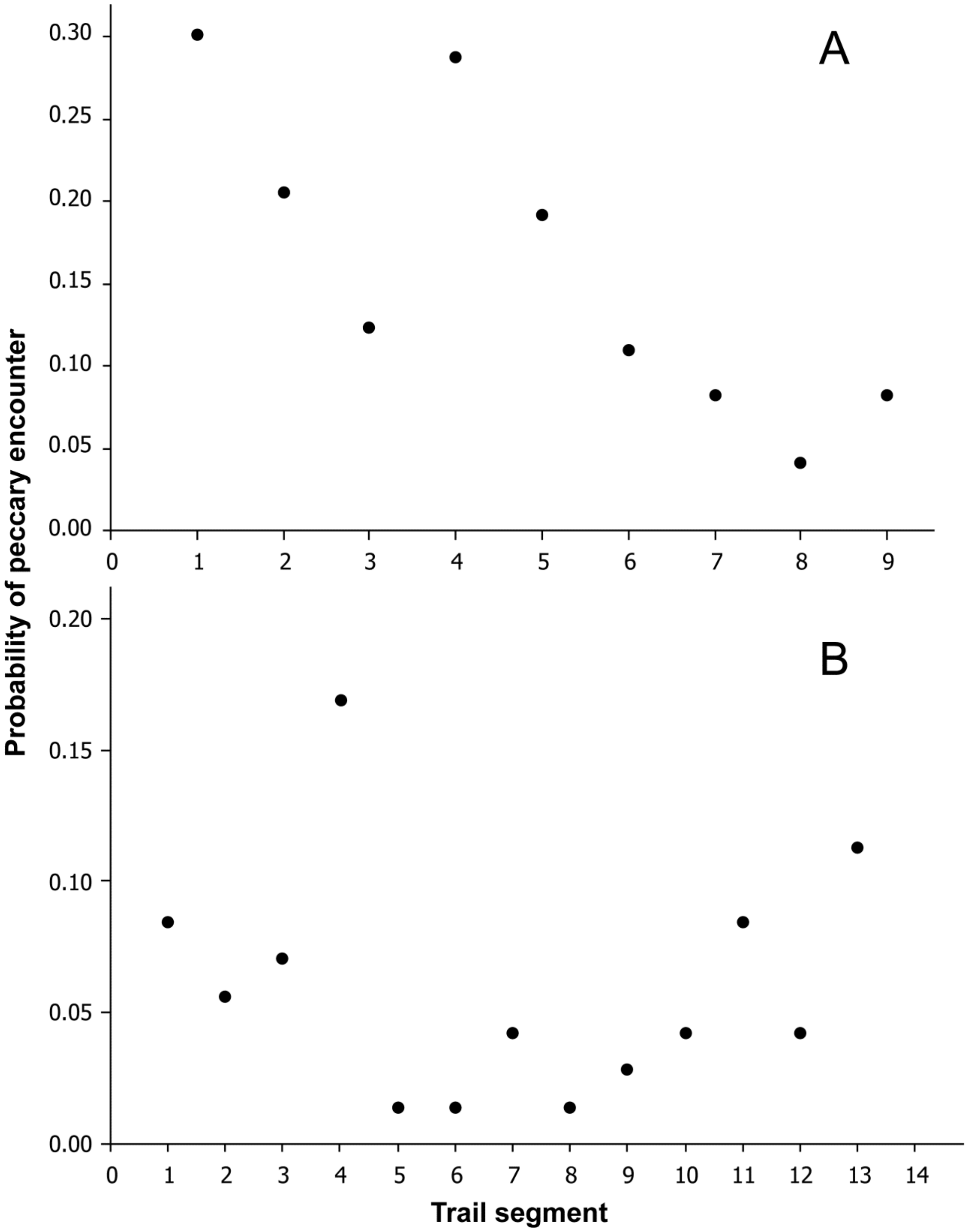

Figure 2.4—Probability of encountering at least 1 peccary for each 300 m trail segment throughout the entire study for A) Trail 1, and B) Trail 3.

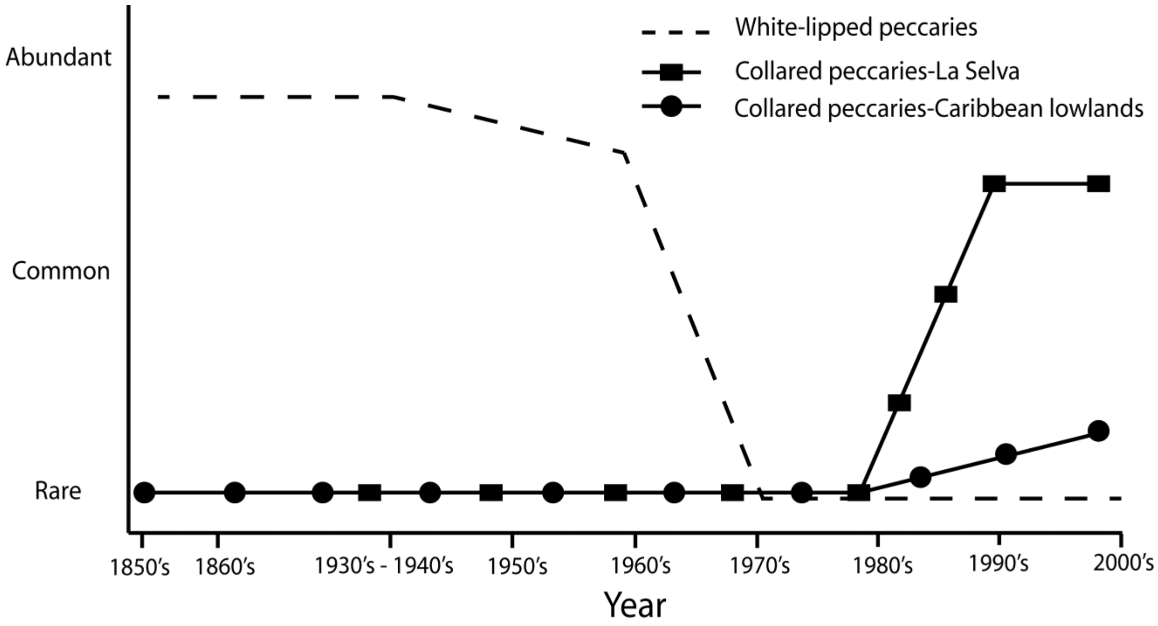

Figure 2.5—Reconstructed hypothesized changes in the abundances of white-lipped peccaries and collared peccaries in the Caribbean lowlands of Costa Rica and La Selva Biological Station based on historical literature and interviews (provided in Table 2.2).

Table 2.1—Estimates of group and individual density with associated standard errors for each diurnal trail.

Trail	Density of Groups (#/km^2)	SE of group density	Density of individuals (#/km^2)	SE of individual density
1	20.66	1.855	65.92	8.29
2	3.73	0.949	21.05	6.96
3	8.27	1.164	38.72	6.75
4	4.25	0.886	19.05	5.78

Table 2.2—Quotes illustrating historical and current peccary populations in the Caribbean lowlands. Citations demarcated with an asterisk (*) are based upon our correspondence with the observer. The text provided herein for Isaías Alvarado-Díaz represents our translation from his original Spanish. With the quotes used here, we remain faithful to the observers' wording and ideas, although some text that they provided is omitted for clarity, focus, and space concerns. Local names in Costa Rica for white-lipped peccaries are cariblanco and chancho de monte and to a lesser extent javali. Waree (variously spelled as wari and wuari) is the name used throughout Nicaragua for white-lipped peccaries and Carr uses that name for his observations of Tortuguero in extreme northeastern Costa Rica. Saino is the name used throughout Costa Rica and Nicaragua for collared peccaries.

Observer or citation	Quote
Squire (1855:281–224) 1850's	"Among the wild animals most common in Central America, is the peccary [*P. tajacu*]…best known by the Spanish name Savalino. There is another animal, something similar to the peccary….called Javalino by the Spaniards, and Waree [*T. pecari*] by the Mosquitoes….swarm all over the more thickly-wooded portions of the country….They go in droves, and are not at all particular as to their food, eating ravenously snakes and reptiles of all kind. They have also a rational relish for fruits..."
Alston (1879–82:110) 1860's	"In Costa Rica, Dr. v. Frantzius informs us that the White-lipped Peccary is found in great droves in the thick primeval forests of the warmer lowlands, but is also met with occasionally in the higher-lying mountain-woods, as at Cariblanco, near the Sarapiqui."
Belt (1874:30) 1860's	"Soon after we heard some wild pigs…or Wari [*T. pecari*]…one of the boatmen leaping on shore soon shot one….These Wari go in herds of from fifty to one hundred."
Slud (1960:76) 1950's	"Ominous are the clopping, champing noises of a herd of White-lipped Peccaries; unsettling is the heavy, growling 'woof' of a startled individual close at hand….Mammals, except agoutis, squirrels, tayras, and monkeys are seldom to be observed"
Isaías Alvarado-Díaz 1930's–2012	"El saino was one of the most hunted. There was a time when the 2 types were there, what they call the 'chancho de monte, el carablanco', the big one, which was found in large herds, but already in those time periods, of the 1980's, there weren't any in this area, those had become history. What there was a lot of was the saino, the little one, the one that now is very abundant at La Selva. What happened was that when they acquired an area that was abandoned pejiballales, then there, with that lost crop, they reproduced tremendously, and now there's a lot. That was one of the animals [the saino] frequently hunted, even though it was less commercial than the tepezcuintle [*Cuniculus paca*]….it was more for use at home, but yes, it was looked for often. The cariblanco was hunted a lot,

I was still able to hunt some sometimes, but they were very easy to hunt because their herds were too big. I was told there were herds of cariblancos of surely more than 100 animals. Because, even my father, told me that they got to kill, let's say 3 to 4 cariblancos, but they had to kill them and leave, until the herd a while later left there, to go get them because nobody dared get close to where those animals were. It was an enormously large quantity of animals, but there was also a tremendous amount of hunting pressure.

When La Selva started being "La Selva", there were already none of those. There were more historically. I think that in the years, what, 1950's maybe, or something like that, there were already too few herds. A small herd, that arrived from that side of the Río Tirimbina and Bijagual, there I was able to see them sometimes, and I was able to hunt sometimes a piece each time I found them. But I already was never able to find a herd of those, no no, they were almost the same as the sainos, they would sense you and would leave. The herds were already very small, diminished, and thus, they were not as aggressive….One of those herds, that you suppose is over 100 animals, travels kilometers…they would rummage, and eat, and that would be noticeable on the [forest] floor….So they were big, enormous, but with this issue of the Braulio Carrillo, or wherever, months could go by where we wouldn't see tracks of cariblancos. But when they appeared, then the quantity was too much….The sainos were hunted for their meat…but many said they didn't like the smell…but I made a well-cooked saino and it is a delicious meat…People, this is what was told to me, hunting cariblancos you could find them together with the jaguar….There were cases where people would shoot, kill cariblancos, but maybe there were 3 hunters and 5 cariblancos were killed, so, they would leave 2 in the water…to go the next day, and the following day when they went, the jaguar had already taken and eaten one. My father would tell me that you'd have to go, shoot, and return to reload, and there was a big rock, and he would go, shoot, and get on top of the rock to reload the rifle, and he went, and jumped on the rock and the jaguar also jumped on the rock, and the animal [jaguar] left, but they both went to the rock to defend themselves, because it seems that a jaguar doesn't hunt a cariblanco in between those huge herds….Of the commercial skins, it was the sainos. In that timeperiod, when people still hunted the sainos a lot and would extract the skin, and would sell them, the closest area where there were leathergoods shops, where they would process leather was Venecia in San Carlos. But not the cariblancos….They [skins] were used to make knife covers, belts, many things, but it was completely commercial….They were used for other things like self defense, if your neighbor's cattle came over to your property, one would grab hair of cariblancos or sainos and burn them and the cattle would leave the area, because for some reason cattle are scared of cariblancos, but tremendously scared…. In the 1930's the cariblanco was shot with a rifle and gunpowder. In La Virgen around 1945 there was a plantation of an African plant for the oil, about 800 hectares, and a great herd of cariblancos got into the field. My father and his colleagues killed them and they took them home. I remember my father coming

	home from work that day riding a horse with a cariblanco laid across the horse. In the 1980's there were only small groups of cariblancos, ~15. The saino and the cariblanco have similar diets. The saino, the little one, one could make the mistake to think there are too many. There aren't any in the Braulio, 85% of the sainos of Zurquí are in La Selva. (pers. com. 26 Feb. 2012)
Daniel H. Janzen* 1963–1970's	"What I recall in 1963–1968 is that La Selva (called Holdridge's finca back then, had lots of javali [*T. pecari*], which I had never seen before (other than in Osa in 1965)….I have no plus or minus memory of collared peccaries [*P. tajacu*]. There was an original station keeper "Rafa" and botero who also talked about them [*T. pecari*], as being a nuisance and common. I spent a lot of time in the La Selva forest back then picking up *Pentaclethra* seeds and other stuff…and I remember how the javali churned up the litter where they had passed. Then maybe about the early to mid 1970's, I recall the comment that the javali were disappearing (or had disappeared) and how strange." (pers. com. 7 Sept. 2011)
Carr (1967:75)	"The other regular turtle eaters on the Bogue beach are…the ravening hosts of wari, or white-lipped peccaries….The gangs of wari range from twenty to a hundred or more. They are direfully efficient scourge of all small animals. Where peccaries pass there are almost no small ground-dwelling animals to be found. Wari are so devastating that when I am asked why the green turtle chooses Turtle Bogue to cling to, out of all the thousands of miles of Caribbean shore that look like good turtle beach, I think first of saying: because peccaries find it hard to get there across the lagoon."
Richard K. LaVal* 1968–1990's	"Once when I was doing the bat study at La Selva (1973–74), I saw a single white-lipped peccary near the trail. Never saw others or any collared during that year. Nor do I remember ever smelling peccaries there. During the OTS course in 1968 we neither saw nor smelled them, nor did people there ever mention the existence of peccaries. By the time I began making regular trips there with the course, in the early 90's, the collared group was there." (pers com. 4 Sept. 2011)
Paul S. Foster* 1971	"…the last known group of about 20 individuals [*T. pecari*] was shot in 1971 in a low area where they would bathe just northwest of the Reserve [Bijagual]. The common name for them around here is cariblanco – also the name of a town up the hill on the way to Vara Blanca." (pers. com. 7 Nov. 2011)

James H. Beach* Late 1970’s	“….(ca. late 1970’s) they were the big ones [*T. pecari*]….The smaller species [*P. tajacu*] are tiny compared to the big mammoth ones, which would scare the bejezus out of you if you snuck up on them - if for some reason you had no sense of smell and you COULD sneak up on them. I remember [someone] running full speed down the loop trail one day, scared out of her whits that the big peccaries were after her….One time, it might have been that one, or another day, they were hanging around the *Carapa* tree eating the fruits (judging by their presence in the immediate area (snorts and snapping branches) and the mess in the mud and torn about shells and missing seeds, and smell). As I recall *Carapa* only had mast fruit episodes in irregular years and that year was one. That *Carapa* tree was on the far loop trail, about 1/4 of the way out where the trail crossed a small stream (*Sabalo esquina*?)….I only saw them at the *Carapa* once.” (pers. com. 19 Mar. 2012)
Deborah A. Clark* 1980’s	“…through most of the 80’s, seeing a group of even so few as 4 Collard Peccaries was a big deal. To the point you’d report it at meals, etc., as a special thing. Most days you’d see none, and there were NO WALLOWS on the forest floor. Then, there was an abrupt explosion of piggies, and in my memory is it happened ca. 1988–89 (?). All of a sudden (it seemed) there were more sightings and growing groups size. Eduin Paniagua, the Forest Guard at the time, came to us all preoccupied, saying the pigs were ruining the forest and that they needed to be culled back to ‘normal’ (for him) levels. We presumed this was due to finally getting illegal hunting down in the reserve, but of course there are no data on either to test this. And this is when pig-wallows began to appear on the forest floor.” (pers com. 8 Oct. 2011)
Amos Bien* 1963–2010	“When I was at La Selva from 1977–81, I never saw a single peccary of any type. I saw rare tracks. On recent visits, La Selva gave me the impression of being overrun by collared peccaries in small groups. Up the hill, at el Plástico - Rara Avis [500–700 m], the story is different: - The prisoners I interviewed told me that they would sometimes shoot the abundant white-lipped peccaries from the balcony while they were there from 1963–65. - From my arrival there in 1983 until the early 1990s, I would see occasional tracks, of collared peccaries I assumed, because the tracks were always only one or two individuals. - However, in 1993, I saw a pair of white-lipped peccaries close-up in broad daylight on the road into El Plástico. We have had no further sightings. - However we have frequent and growing sightings of collared peccaries, although subjectively much less abundant than at La Selva. There are abundant tracks of single individuals or pairs, but not of herds. I cannot tell apart the tracks of the two species. A camera-trapping project at Rara Avis last year [2010] also captured collared, but not white-lipped peccaries.” (pers. com. 2 Nov. 2011)

Gary S. Hartshorn* 1970–1980's	"My earliest recollections are from my long-term stints (usually ten days straight at LS, then four days home in SJO) during 1970 and the first eight months of 1971. During my post-doc research on gaps (1972–1975), I typically spent four nights at LS and three at home. Post-1975 till my 1989 move to DC, I typically was at LS several days per month. The long-time foreman, Rafael Chaverria (that OTS inherited from prior owner Les Holdridge), was my foremost teacher of local natural history. I regularly talked with him about trees as well as wildlife; he was an excellent observer and woodsman. I recall him being excited to tell me (in the early 70s) that he saw the tracks of a sizeable herd (>20?) of white-lipped peccaries ("cariblancos") where they had crossed the far-side of the Loop Trail. I asked him how he knew they were cariblancos, not "sainos" (= collared peccaries)? He said by the size of the hoof-prints and that there was no odor so typical of collared peccaries. Also, that he had been a hunter and knew well the habits of cariblancos. Interestingly, an older boatman (Manuel Maria) based in Puerto Viejo also told me stories about hunting cariblancos in the swamps of what is now LS. According to these knowledgeable hunters, cariblancos moved in fairly large herds over sizeable geography, possibly migrating into the lowland swamps to feed on *Carapa nicaraguensis* (old name = *C. guianensis*) seeds. In the 70s and probably most of the 80s, collared peccaries were rather rare at LS. I might smell or see them just a few times per year. In the 70s we would occasionally hear shots (rifle or more typically shotgun) at night and assumed they were by poachers. I'm just speculating, but the abundance of squatters/hunters behind LS (i.e., in what became the Zona Protectora LS) may have been a factor in the low abundance of peccaries (both species?) at LS in the 70s. It wasn't till the late 80s with the consolidation of Greater La Selva and more effective patrols (e.g., Edwin Paniagua—another "reformed" hunter) that sainos became more abundant and noticeable in the front of LS. It wasn't just the lab clearing, but also sainos were quite noticeable in the Las Vegas annex (Bob Hunter's farm). If I recall correctly, sainos have been frequently seen along the first half of the STR since the latter 90s. In setting up the altitudinal transect from LS to Volcán Barva (mid-80s) I remember encountering wallows in the muddy sections of the transect trail between 500 m and 700 m. Most importantly, there was no saino odor near these fresh wallows. Edwin Paniagua agreed with me that they were cariblanco wallows. But, to my knowledge, we never had any confirmed sightings of cariblancos along the transect trail." (pers. com. 2 Nov. 2011)
Don E. Wilson* 1968–1970's	"...we had no sightings of cariblancos on the transect during our early surveys of the ZP. I also never saw peccaries of any sort at La Selva in the early days. I first went in there in dry season of 1968. I also don't recall peccaries of any sort in there in 1970–71." (pers. com. 2 Nov. 2011)
F. Gary Stiles* 1960–1980's	"I never saw white-lips at La Selva, and not very many collared peccaries either. I recall several encounters in the late 1960s when I was working 'way out the Central Trail…and only a few encounters in the early 1970s when I was spending most of my time at La Selva. On several occasions I ran into hunters with dogs towards the back of

	the property, and I suspect that the population was quite low…as I recall, I never saw any group larger than 3–4 animals. My visits to La Selva in the 1980s were more sporadic, often associated with OTS courses. I do recall seeing two groups of around 6 on one visit in the late 1980s, one out the East Boundary and one on the Central Trail (I suppose it could have been the same group, no way to tell but the distance between the encounters was probably ca. 500? m). I remember this because one of the groups was relatively aggressive (I was considering finding a tree!), in sharp contrast to my encounters in the 1970s, when the peccaries were invariably very skittish.” (pers. com. 12 Sept. 2011)
Joseph Wunderle* 1970’s	“I first went to La Selva in January 1973, and then on followup trips (1979), but do not recall seeing peccaries (either species). Heard some and saw some footprints and digging evidence in 1973, but do not know which species.” (pers. com. 7 Dec. 2011)
David Janos* 1973–late 2000’s	“When I lived at La Selva from 1973 to 1975, I very rarely encountered any peccaries. Only one encounter sticks in my mind, and that was just two small collared peccaries one of which got a bit aggressive with me. I’ve never seen a cariblanco or anything that I recognized as a sign of one at La Selva or on the transect. My impression is that as collared peccary abundance increased at La Selva through the ‘90s, it also increased in the lower reaches of the altitudinal transect (especially below 1070 m). I can’t remember when, but perhaps in the ‘90s I was walking on the west bank in the second growth over towards Tosi’s house, and ran into a huge herd of what might have been 20–30 animals (including young). Also, sometime in the late 2000s I was out near the end of Sendero Sarapiquí when I came upon a mama saino and two babies that weren’t any bigger than American footballs. I recall Rafael Chaverria telling me that when he was a young man he hunted cariblancos in the La Selva swamp. I agree with Gary that the most likely explanation for the disappearance of cariblancos from La Selva pre-OTS, and perhaps the low numbers of sainos in the ‘70s most likely was hunting pressure especially at the back and around the edges of La Selva.” (pers. com. 23 Nov. 2011)
Mirjam Knörnschild* 2000’s	I have seen peccaries crossing the bridge several times [a ~1.5 m wide, ~100 m long walk bridge crossing the Río Sarapiquí] …always from the comedor [dining room] side to the lab clearing side…I don’t know whether me sitting close to the lab clearing side prevented them from crossing both ways—they always seemed to be genuinely surprised to find someone sitting in their way. Twice, I got up and let them pass because they couldn’t muster the courage to squeeze by…the rest of the times they walked past right behind my back. I always thought it must have been part of the group that hung out at the lab clearing because they were so habituated. The group that crossed the bridge was rather small (once, it was only 4 peccaries; the rest of the times there were around 6–8 peccaries). They crossed the bridge between 4:30 and 5:30 a.m., always when it was still dark.” (pers. com. 12 Dec. 2011)

Table 2.3—Estimated mean group size, largest group observed, and the prevalence of singletons for collared peccaries in various parts of its range. NR = not reported. ([a]) denotes as cited by Sowls 1997.

Location	Mean group size	Largest group	Singletons	Citation
Costa Rica:		19	34.4%	Current study
Singletons	3.94			
No singletons	5.48			
Argentina	5.4 23.2 3	12 50 5	NR	Altrichter 2005
Brazil	9	NR	NR	Keuroghlian and Eaton 2008
Brazil	4.3	10	NR	de Azevedo and Conforti 2008
Brazil	9	NR	NR	Keuroghlian et al. 2004
Mexico	3.3 4.5	12	Groups of 1–4 commonest	Mandujano 1999
Panama	3.1	NR	44%	Robinson and Eisenberg 1985
Peru	NR	NR	42%	Kilte and Terborgh 1983
Venezuela	6.5	NR	29%	Robinson and Eisenberg 1985
Arizona	8.5	53	4 instances	Knipe 1957[a]
Arizona	8.6	NR	NR	Day 1985[a]
Arizona	12	NR	NR	Day 1985[a]
Arizona	7.9	NR	NR	Sowls 1984[a]
Arizona	11.2	NR	NR	Byers and Bekoff 1981[a]
Arizona	8.8	19	No	Byers 1980[a]
Arizona	8.1	18	NR	Bigler 1974
Texas	5.47	NR	NR	Green et al. 2001
Texas	4	NR	27%	Gabor and Hellgren 2000
Texas	14.4	27	No	Bissonette 1982[a]

Table 2.4—Estimated densities for collared peccaries in various parts of its range as cited by: [a] Sowls 1997; [b] Harvenson et al. 2000; [c] Keuroghlian et al. 2004; [d] Naranjo and Bodmer 2007.

Locality	Density (individuals/km^2)	Citation
Costa Rica, La Selva	14±1	Torrealba and Rau 1994
Panama, Barro Colorado Island		Willis unpublished
1983–2010	6–35	
2006–2011	18–25	
Panama, Barro Colorado Island	~1–35	Wright et al. 1999
Gigante	~1–12	
Panama	0–7	Wright et al. 2000
Panama, Barro Colorado Island	16	Eisenberg 1980[a]
Panama, Barro Colorado Island	9.3	Glanz 1982
Brazil, Pantanal, Matto Grosso	0.78	Schaller 1983[a]
Brazil, Caetetus Ecological Station	2.8–8.9	Keuroghlian et al. 2004
Brazil, Caetetus Ecological Station	4–15	Cullen 1997[c]
Brazil	1.9–11.6	Peres 1996
Guatemala, Hunted	2.38	Novack et al. 2005
Unhunted	8.12	
Mexico, Chamela Biological Station	4.9 ± 1.6	Mandujano 1999
Mexico, Lacandon Forest	1.15–1.53	Naranjo et al. 2004[d]
Mexico, Chamela	4.1–10.7	Mandujano 2007
Peru	5.6	Emmons 1987[a]
Neotropics	12	Robinson and Redford 1986[a]
Peruvian Amazon	3.3	Bodmer 1989[a]
Venezuela, Hato Masaguaral	8.5	Eisenberg et al. 1979[a]
Venezuela, Hato Piñero	7.5–17	Polisar et al. 2008
Venezuela, Hato Piñero	7.5	Scognamillo et al. 2003
Arizona	4.5–11.5	Schweinsburg 1971[a]
Arizona	3–4.7	Day 1985[a]
Arizona	2.1–4.5	Supplee[a]
Texas	3.8–8.8	Low 1970[a]
Texas	3.3–11	Bissonette 1982[a]
Texas	2.01–9.15	Gabor 1997[b]; Ilse and Hellgren 1995[b]
Texas	8.4–10.3	Gabor and Hellgren 2000

CHAPTER 3

FOREST FRAGMENTS AND RODENT ABUNDANCE AND DIVERSITY IN COSTA RICA'S CARIBBEAN LOWLANDS

Abstract

The ability of low-density rodent communities to sustain connectivity and viable populations in fragmented landscapes is important to maintain natural processes in lowland rainforests. We conducted live-rodent trapping from 2007 to 2010 in May through September in 15 forested areas in the Caribbean lowlands of Costa Rica to test for differences among fragments. We found trap success to be quite low in the area (1.08% for all captures), and highly variable among fragments, but not for the same area among years. The composition of species caught was also quite variable, with some areas dominated by spiny pocket mice (*Heteromys desmarestianus*), and others by dusky rice rats (*Melanomys caliginosus*) and Tomes' spiny rats (*Proechimys semispinosus*). Although regressions for nightly trap success and fragment variables such as area size, perimeter, perimeter-to-area ratio, and elevation maximum and minimum did not present reliable results, nightly trap success for all species, and for spiny pocket mice only, were higher in larger (> 9 km^2) than in smaller fragments. Sex ratios for spiny pocket mice did not differ from 1:1 over the lowlands, and did not appear different in small and large fragments. Male and female mass for this species differed significantly, whereas mass for each sex was not significantly different among large and small fragments. Habitat fragmentation and degradation in this area are relatively recent, and the consequences of this habitat alteration may not be fully evident at this time. Some population differences can be attributed to fragment size, yet this complex matrix of forest fragments is still valuable in a conservation context.

Introduction

The Neotropics are one of the most species-rich areas of the world, and unfortunately, have experienced high levels of landscape change and alteration by vegetation clearing and other sorts of anthropogenic modification. Landscape change in the form of deforestation has increased with the advent of agribusiness, industrial forestry, and waves of colonization (Bierregaard et al. 1992). Habitat fragmentation and degradation remain the most serious threats to global biodiversity (Vitousek et al. 1997, Sánchez-Azofeifa et al. 1999, Pimm and Raven 2000, Sala et al. 2000), yet in an increasingly fragmented region, a landscape of forest patches may represent the only viable habitat remaining for organisms and conservation.

Though habitat fragmentation has been the focus of much research, the biological and physical effects of fragmentation are poorly understood (Harrison and Bruna 1999, Fahrig 2003, Ewers and Didham 2007), particularly in tropical ecosystems (Fahrig 2003). Our understanding of the effects of landscape change to animal populations is biased by an inordinate amount of data from non-tropical systems, the responses of which may not be representative of lowland tropical rainforests, given the diversity, continuous growing season, food web dynamics, and stronger negative edge effects in the tropics (Laurance et al. 2002, Fahrig 2003).

The Sarapiquí region of Costa Rica, situated in the northeastern part of the country encompassing the vast majority of the Caribbean lowland tropical forests, was extensively forested, even into the 1970's. This area has been subject to considerable habitat degradation and fragmentation in the past several decades. From 1976 to 1996 forest cover in the region decreased from 55% (513 km^2) to 34% (313 km^2) and the number of forest fragments increased from 537 to 1231 (Sánchez-Azofeifa et al. 1999), with 80% of forest fragments in the area being smaller than 10 ha (Bell and Donnelly 2006).

Small mammals are important components of Neotropical systems and play a critical role in the complex interactions of tropical food web systems as predators of fruits, seeds, and invertebrates. Rodents are key post-dispersal seed predators of many plants and can remove a large proportion of seeds beneath parent trees or from mammal scat, ultimately affecting the demography and composition of plant communities (Sánchez-Cordero and Fleming 1993, Brewer and Rejmanek 1999, Mangan and Adler 2002, DeMattia et al. 2006, Hanson and Brunsfeld 2006). Additionally, small mammals are important prey items for larger carnivorous mammals, reptiles, and predatory birds. The Caribbean lowlands of Costa Rica have low-density, small mammal communities. Our current understanding of the effects of fragmentation on biodiversity in the Caribbean lowlands has focused on herpetological and ornithological taxonomic groups (Bell and Donnelly 2006, Sigel et al. 2006), and little is known about the population dynamics and effects of habitat fragmentation on low-density, albeit ecologically important, rodent communities.

The potential negative effects of habitat fragmentation and degradation include declines in species diversity and abundance, decreased genetic diversity, and changes in species composition and demographic parameters (Saunders et al. 1991, Turner 1996, Laurance et al. 2002, Fahrig 2003). For mammals, no clear trends exist between densities and patch size (Bowers and Matter 1997). Rodent communities do not have “typical responses” to habitat fragmentation, highlighting that landscape changes can affect species differently. For instance, in temperate forests rodent communities overall show positive responses to clear-cutting (Kirkland 1990), though species-specific responses can differ (Lomolino and Perault 2000, Nupp and Swihart 2000). In the tropics, a negative relationship between fragment size and rodent abundance and richness is often observed (Laurance 1994, Vieira et al. 2009).

Habitat fragmentation can also affect a suite of population attributes such as sex ratios and individual mass. Fragmentation can affect food resources, predation, competition, and dispersal in a species-specific manner. Sex ratios and physical condition have been shown to be affected by fragment size for many animals (Dantas et al. 2009, Díaz et al. 1999, Diffendorfer et al. 1995, Nupp and Swihart 1996). Sex ratios are predicted to be altered from the "normal state" in forest fragments if anthropogenic activities are affecting any of the ecological, behavioral, or evolutionary factors that ultimately determine this ratio (Dantas et al. 2009, Frankham 1995, Seger and Stubblefield 2002). If habitat fragmentation has a negative effect on the food resources of a species, it is predicted that physical condition, often measured by body mass, will decrease (Díaz et al. 1999, Nupp and Swihart 1996).

Herein, we explore the effects of forest fragmentation on small rodent communities in the Caribbean lowland rainforests. Our specific aims are to: 1) provide an overview of relative abundance and diversity of all species in a variety of fragment sizes, 2) test how landscape metrics, such as elevation, fragment size, and the interaction between fragment perimeter and area affect relative abundance,3) test how relative abundance varies across years for spiny pocket mice, and 4) test if fragment size affects sex ratios and mass of adult spiny pocket mice.

Methods

We trapped rodents in 15 sites in northeastern Costa Rica (Fig 3.1). The Caribbean lowlands of Costa Rica have similar temperatures throughout, although annual precipitation can vary from 2.4 m to 4.8 m per year; La Selva Biological Station itself receives 4 m annually. For a detailed description of the ecological history and biology of the Caribbean lowlands see McClearn et al. (in press). The sampled sites varied in their size, degree of isolation, and degree of anthropogenic disturbance (Table 3.1).

We trapped in the years 2007–2010, typically May through September. We trapped approximately 7 consecutive nights at each site, and generally once per site, although 7 sites were surveyed multiple times to test if sampling across years was comparable. At these sites we compared nightly trap success for spiny pocket mice. We created a boxplot for these 7 sites by year, and when appropriate performed Mann–Whitney U tests (Fig. 3.2). Because we found no significant differences across years for nightly trap success, we are confident that we can compare all sites across all years. We trapped using either a grid pattern, or trap lines (Table 3.2). Grid trapping consisted of 90 Sherman live traps (8 cm × 9 cm × 23 cm; H. B. Sherman Traps, Inc., Tallahassee, FL) and 10 Tomahawk traps (49 cm × 7 cm × 7 cm; Tomahawk Live Trap Company, Hazelhurst, WI) placed on a 19 m × 4 m grid, each 1 m apart. The trapping grid was left in place for 7 nights, checked each morning, and traps rebaited. Due to low trap success and inability to produce precise population estimates with this method, we began to sample sites using trap lines. Traps were placed in a variety of areas to maximize trap success—for example, inside hollow logs, under and next to logs, in areas with dense understory, and in a variety of terrains. Traps typically remained in the same place for 3 nights, and then were moved to new locations within the same site thereafter. Only Sherman live traps were used, and they were checked, and rebaited each morning. Bait was a mixture of corn, quick cooking oats, and bird feed that contained a variety of seeds. When a rodent was captured, we collected data on the species, sex, mass, and uniquely marked each individual by removing part of a toe. All animals were released in the same area where caught. Although transect and grid-trapping methodology can produce different trapping results (Pearson and Ruggiero 2003), we included data from both methodologies because including the grid data allowed us to expand the number of fragments sampled, and when we repeated the analyses excluding the grid-trapping data the overall results and patterns remained the same.

Geographic information, including area, perimeter, and lowest and highest elevation for each fragment was calculated using a combination of Google Earth Pro and ArcGIS 10. Layers for ArcGIS were obtained from the La Selva GIS database (http://ots.ac.cr/index.php?option=com_wrapper&Itemid=352). Fragments were delineated based on continuous coverage of canopy tree crowns. Fragment boundaries were delineated at any areas smaller than 2–3 tree crowns, and any other large boundary visible on landscape imagery, such as large rivers, agricultural fields, pastures, and roads. For La Selva, we included only the measurements within the main property boundaries, although it is connected to a larger tract of high elevation forest, Parque Nacional Braulio Carrillo (Fig. 3.3). We partitioned the data into nightly trap success for unique individuals of spiny pocket mice (*Heteromys desmarestianus*), and did regressions between nightly trap success and fragment area, perimeter, maximum elevation, lowest elevation, and perimeter to area ratio. Because of problems with the residuals for the significant regressions, we tested for nightly trap success differences among all the sites using a Kruskal–Wallis test. We re-ran this analysis only with sites where spiny pocket mice were captured. The Kruskal–Wallis test showed significant differences in trap success among sites, yet the test does not allow us to identify the individual sites that produced these differences. For these reasons, we created a histogram of all fragment areas and partitioned the data set into 2 size categories—large fragments greater than 9 km^2 (La Selva, Juan Enriques, Maquenque) or small fragments smaller than 9 km^2 (Starky, Agrícola Sofía, Dole, Chiquita, Nogal, La Guaria, Water Tower, Selva Verde, Frag A, Tirimbina, Río Frío, Berlin) (Table 3.1). We then did a Mann–Whitney U to determine if nightly trap success for spiny pocket mice, and all rodent species combined, differed in large and small fragments.

We used a Chi-square test to examine if the sex ratio of spiny pocket mice for all years, and all sites combined deviated from a 1:1 ratio. We were interested in determining if sex ratios in small and large fragments differed, but with only 3 large sites, we restricted our analysis to creating a boxplot of the ratios for the two groups; large fragments included Juan Enriques, La Selva, and Maquenque, whereas the small fragments included Selva Verde, Tirimbina, Agrícola Sofia, Starky, Water Tower, and Frag A. To test if mass was significantly different among adult males and females, we used a Mann–Whitney U test. Juvenile and adult pelage for this species is quite distinct, and any individual with some amount of juvenile pelage was omitted from the analysis. All recaptured individuals were only included once in the analysis, with the mass of the first day of capture. We also tested if female mass or male mass differed in the various fragments. We combined data for the same sites from different years, and used sites with 5 or more individuals. For females we tested differences between La Selva, Agrícola Sofía, Juan Enriques, Maquenque, Selva Verde, Starky, Tirimbina, and Water Tower, whereas we tested differences in males in La Selva, Agrícola Sofía, Maquenque, and Starky. These statistical tests were run in Minitab 14. This project was undertaken with the approval of the University of Kansas Institutional Animal Care and Use Committee. All animal handling protocols were in accordance with the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Results

Overall trap success for unique individuals in all sites combined was 0.81%. Trap success including recaptures was 1.08%. Trap success varied by site with Tirimbina and Selva Verde having the highest values, and La Guaria the lowest with no rodent captures (Fig. 3.4). The overall trap success for La Selva was 1.22 and 1.078%, for all captures and unique individuals only, respectively. Trap success in La Selva during different years yielded similar results—1.67 and 1.28% in 2007 and 2008, respectively. When focusing only on spiny pocket mice, nightly trap success was not significantly different among years for each of 7 sites that were sampled over multiple years (Juan Enriques $U_{7,15} = 71$, $P = 0.56$; Agrícola Sofía $U_{7,10} = 75$,

$P = 0.26$; Starky $U_{6,19} = 60$, $P = 0.27$; Water Tower $U_{10,13} = 126$, $P = 0.73$; La Selva (years 2007 and 2008) $U_{21,33} = 654$, $P = 0.18$; Nogal and La Guaria had 0 captures for each year; Fig. 3.2). Conversely, trap success varied in the same year at different sites. The species composition of each site was different, and we did not capture all species surveyed at any single site.

Heteromys desmarestianus (hereafter referred to as spiny pocket mouse) was the species caught in the majority of plots. Overall, trap success for spiny pocket mice was 0.82 and 0.62% for all captures and unique individuals, respectively. Highest trap success was in Selva Verde, and no individuals were captured in La Guaria, Nogal, Chiquita, Dole, and Río Frío (Table 3.2).

Area of our sampled fragments ranged from 0.29–17.3 km^2. The mean and median fragment sizes were 3.93 km^2 and 1.82 km^2, respectively. Regression analyses of nightly trap success for spiny pocket mice and area ($F_{1, 224} = 2.24$, $P = 0.136$) and perimeter ($F_{1, 224} = 1.18$, $P = 0.279$) were not significant. Significant regressions were found for trap success versus perimeter-to-area ratio (Nightly trap success = 0.0108 – 0.000772 × perimeter-to-area; $R^2 = 6.1\%$, $F_{1, 224} = 14.60$, $P < 0.001$), minimum elevation (Nightly trap success = 0.00458 + 0.000053 × minimum elevation; $R^2 = 3.3\%$, $F_{1, 224} = 7.72$, $P = 0.006$), and maximum elevation (Nightly trap success = 0.001 + 0.000054 × maximum elevation; $R^2 = 7\%$, $F_{1, 224} = 16.83$, $P < 0.001$). Although superficially significant, all 3 of these regressions had small R^2, and the residuals were not-normally distributed, making the statistical significance of these regressions questionable. No non-linear patterns were obvious when we explored the scatterplots and residual plots. Nightly trap success for unique spiny pocket mouse captures differed among all sites surveyed ($H_{13} = 80.39$, $P < 0.001$), and among all sites where this species was present ($H_9 = 58.89$, $P < 0.001$). Significant differences were found in small versus large fragments for nightly trap success of all species ($W_{86, 140} = 10891.5$, $P = 0.0136$, large fragment median = 0.0094, small fragment median = 0) and for spiny pocket mice only ($W_{86,\,140}$ = 10979.5, P = 0.0054, large fragment median = 0.0052, small fragment median = 0).

The total number of male and female spiny pocket mice captured in all years combined did not differ significantly from a 1:1 sex ratio (χ^2_1 = 1.438, P = 0.231). Due to sampling only 3 large fragments, we were constrained to only visually inspect boxplots for large versus small fragment male:female sex ratios. There were no observable differences for sex ratios in the small and large fragments (Fig. 3.5). Overall, adult males weighed significantly more than adult females ($W_{76,\,97}$ = 8625.5, P < 0.001). Adult males had an average mass of 82.05 g (*SE* = 2.20 g, median = 86.5 g, range = 33–115 g), whereas adult mean female mass averaged 67.64 g (*SE* = 1.18 g, median = 67, range = 31–100 g). Mass of adult females was not significantly different among the following sites: La Selva, Agrícola Sofía, Juan Enriques, Maquenque, Selva Verde, Starky, Tirimbina, and Water Tower (H_7 = 9.05, P = 0.249). Male mass from La Selva, Agrícola Sofía, Maquenque, and Starky also did not differ significantly (H_3 = 2.87, P = 0.412). Mass of females ($W_{46,40}$ = 2064.5, P = 0.5851) or males ($W_{40,36}$ = 1508, P = 0.7430) did not differ significantly between individuals in large fragments and small fragments.

Discussion

Rodent communities in fragmented landscapes—The proportion at which rodents were encountered differed among sites, with spiny pocket mice (*H. desmarestianus*), dusky rice rats (*Melanomys caliginosus*), and Tomes' spiny rat (*Proechimys semispinosus*) representing the most frequently captured species overall (Fig. 3.4). We are aware that particular species may be difficult to sample with live-traps placed on the ground (Chapter 4), and that utilizing a variety of baits may have allowed us to sample different feeding niches, but if we focus on the species that our trapping effort targeted, ground-dwelling, granivorous rodents, we are able to make general observations on the community composition across sites.

The rodent community in Costa Rica's Caribbean lowlands is sparse, despite several large tracks of forest, and some species may be affected by anthropogenic disturbances. The spiny pocket mouse was the most common species caught throughout the study, although small fragments were typically dominated by other species or had depauperate rodent populations (Fig. 3.4). Overall trap success at La Selva (excluding La Guaria) was 1.67% in 2007 and 1.28% in 2008. Despite large population fluctuations that can occur in densities of small rodents in the Neotropics, particularly after large disturbance events (Klinger 2007, Klinger and Rejmánek 2009, Klinger 2006), yearly trap success and comparison of nightly trap success of spiny pocket mice in plots sampled on multiple years indicate that overall relative abundances were similar (Fig. 3.2). Species composition could fluctuate among years in some of our sampled sites. For example, during our trapping efforts, spiny pocket mice were caught in all 5 trapping sites within the main property boundaries of La Selva. However, multiple captures of long-whiskered rice rats (*Transandinomys bolivaris*) occurred in 4 of the 5 sites in La Selva during 2008 only, and the species was not caught in sampling at La Selva in 2007 or 2010, even in the same areas where it was captured in 2008. These data, although limited, provide interesting information about the likely population fluctuations of long-whiskered rice rats in these lowland forests.

The long-whiskered rice rat is considered an uncommon species found in mature evergreen forests (Reid 2009) and was not captured outside of La Selva during this study. In contrast, the dusky rice rat (*Melanomys caliginosus)* was not trapped at La Selva, though it was found in several other forest fragments sampled. This species is found in more disturbed and altered habitat such as overgrown fields, brushy secondary growth, and forest edges (Reid 2009). In our combined experience trapping at La Selva, we have only caught 1 pregnant individual: it was trapped in the secondary forest annex of La Flaminea, not within the main property boundaries. Within the main property boundaries, this species has been trapped only in edge and severely disturbed forest (Rivas Pava and McCoy Colton 1999).

Tomes' spiny rat (*Proechimys semispinosus*) is a large (> 300 g) echimyid rodent that we trapped in several forests. Adults of this species are not represented in our capture data because the size of our traps only allowed for the capture of juveniles and subadults. Nevertheless, Tomes' spiny rats were captured in several of the sites, although it was much more prevalent in the small fragments. Although we know our trapping efforts did not capture all of the species present in this area, the proportion of each species trapped does provide better insight into the ecology of these forests. Tomes' spiny rat and long-whiskered rice rats can be found throughout the landscape, albeit at higher relative abundances in small and disturbed habitats. When these two species are abundant, spiny pocket mice tend to be at relatively low abundances. Further trapping efforts in the area may elucidate what ecological characteristics allow for these different species to thrive, and if the presence of one species directly limits the abundance of others.

The community composition and relative abundance of species varied across sites, but overall, trap success in the Caribbean lowlands was particularly low. Neotropical sites can vary greatly in trap success; mean trap success across 10 studies was 7.18%, with a range of 1–15.7% (Kelly and Caro 2003). Our results show comparable low trap success as for a deciduous dry tropical forest in Venezuela and tropical moist forest in Belize, that reported values of 1% and 1.3%, respectively (Kelly and Caro 2003). Differences in rodent abundance are likely tied to a multitude of biotic and abiotic factors which are difficult to untangle. Highest abundances typically occur in middle elevations of a species' ranges (McCain 2006), although relatively high trap success of 15.7% has been reported in lowland moist forests in Panama (Kelly and Caro 2003).

Methodological factors, including trap type, grid versus trap-line patterns, and bait can affect trapping results (Weihong et al. 1999, Woodman et al. 1996), but are unlikely reasons for the low relative abundances reported herein. Trap success data can provide reliable estimates of relative abundances at densities lower than 20 captures per 100 trap nights (Brown et al. 1996). The Caribbean lowlands of Costa Rica have a history of low trap success (Janzen and Wilson 1983, Rivas Pava and McCoy Colton 1999, Romero, pers. know.), and thus our results are not an artifact of the methodology used. Although terrestrial rodents are not very abundant in these forests, they still are some of the main handlers of seeds on the forest floor (Rosales Adame 1998), and can exert strong impacts on these ecosystems.

Fragmentation and the spiny pocket mouse—Spiny pocket mice can be common and widespread; in the lowlands they are typically found in mature, wet forests (Reid 2009). This species consumes seeds (especially from palms), fruit, and insects. Spiny pocket mice can be the principal handlers of seeds (Brewer and Rejmánek 1999), even in the lowland Caribbean forests of Costa Rica (Rosales Adame 1998). The spiny pocket mouse is important in Neotropical ecosystems because it acts as a seed predator and can remove a large proportion of certain seeds, and also scatterhoards and caches seeds aiding in dispersal and germination (Brewer and Rejmánek 1999, Brewer 2001, Klinger and Rejmánek 2010, Martínez-Gallardo and Sánchez-Cordero 1993, Sánchez-Cordero and Fleming 1993). We focused the majority of this study on the spiny pocket mouse, because it was caught at most sites, can have large ecological impacts, and may respond negatively to habitat degradation. Indeed we found that fragment size affected the relative abundance of the species. We were unable to trap any spiny pocket mice in some of the smallest fragments and relative abundance was generally lower in small fragments.

Although spiny pocket mice can be one of the dominant rodents in the lowland forest of Central America, the effects of habitat degradation and fragmentation on its populations are not clearly understood (Sánchez-Cordero and Fleming 1993, Klinger 2006). We trapped no spiny pocket mice at 5 sites: La Guaria, Nogal, Chiquita, Dole, and Río Frío. These sites were some of the smallest and most isolated forest fragments surveyed, and many of these fragments are embedded in banana plantations and exposed to pesticide drift from periodic air applications (Romero, pers. know.). In tropical rainforests, isolated and small fragments often suffer from reduction in species richness and have fewer recorded species than larger contiguous forests when the same sampling efforts are applied (Turner 1996). Pesticides and other chemical pollutants can also have large effects on animal populations and are considered agents of global change (Letcher et al. in review.).

Given that we did not trap spiny pocket mice in some fragments, it is not surprising that nightly trap success for this species differed across all surveyed sites. More interestingly, even in sites where *H. desmarestianus* was caught, nightly trap success differed, thus, relative abundances of this species vary across the landscape in the Caribbean lowlands of Costa Rica. Populations in the Caribbean lowlands have been described as stable on a year-to-year basis (Fleming 1974), and we found similar results when we compared nightly trap success for sites that were sampled multiple years. Reported population fluctuations are typically associated with fruit availability and disturbance events (Klinger 2007, Klinger and Rejmánek 2009, Klinger 2006, Klinger and Rejmánek 2010). For example, a flood eliminated a population of 34.4 individuals/ha in Belize, which rebounded to a density of 42.5 individuals/ha 2 months after the flood (Klinger 2007). Other disturbances like hurricanes can affect food resources and survival. A population of 46.8 individuals/ha decreased to 23/ha in a 2 year period, and when food plants began to fruit again the population increased to 77.3/ha (Klinger 2007). Densities for this species across its geographic range can be quite varied (DeMattia et al. 2004). In Panama, the spiny pocket mouse was not as abundant in the lowlands as *Liomys adspersus* and mean monthly density was estimated at 0.67 individuals/ha (Fleming 1970). At La Selva, monthly population estimates in the 1970's ranged from 7–18 individuals/ha, and a total density of 10–18 mice/ha was estimated (Fleming 1974). Densities of 37, 6836, and 1004 individuals/km^2 have been reported in the Maya Mountains of Belize (Caro et al. 2001).

Spiny pocket mice have been described as forest specialists, found in forest interior and infrequently in disturbed areas and edges (Medellín and Equihua 1998, Sánchez-Hernández et al. 2001, Suzán et al. 2008). Conversely, Chinchilla (2009) found that montane spiny pocket mice (*Heteromys nubicolens*) were more abundant in small fragments than in large fragments or continuous forest. Our results indicate that nightly trap success, and thus relative abundances, for spiny pocket mice and all species combined, are higher in large forested areas when compared to the smaller fragments (< 9 km^2). For spiny pocket mice specifically, the graphical representation of our data (Fig. 3.4) suggest that fragments smaller than 9 km^2 are capable of holding populations similar to those we designated large fragments. However, there does appear to be a threshold somewhere between 1.14 km^2 and 1.82 km^2 (areas of La Guaria and Agrícola Sofía) where populations of spiny pocket mice do not do well.

Our regressions are not helpful in predicting patterns and relationships given the problematic residuals and R^2 values, but they suggest that the amount of edge habitat (perimeter:area ratio), and the minimum and maximum elevations in fragments may play a role in the dynamics of these populations. We observed a decrease in nightly trap success with an increase of perimeter-to-area ratio. Rodent responses to edge habitat can be species specific, and these results suggest that spiny pocket mice do not respond well to edge habitat. With the present data we are unable to comment on the mechanisms driving this likely negative response to edges, and further research addressing specific questions about rates of survival and availability of food resources and habitat between interior and edge habitat will help elucidate potential patterns. Elevation also may be a factor that influences these populations. Overall, we observed with both minimum and maximum elevation, that as elevation increased so did nightly trap success. Parts of the Caribbean lowlands (including areas of La Selva) undergo yearly floods and elevation in these fragments may represent an important factor for the survival of these populations.

The ability of spiny pocket mice to move across a fragmented landscape is unclear and can be affected by a multitude of factors. For instance, Burkey (1993) found less seed predation (attributed to fewer seed predators, including spiny pocket mice) and increased egg predation (attributed to more mammalian predators) within 100 m of the forest edge. Here, dispersal to new fragments may be inhibited by aversion to edges or decreased survival in these areas. Furthermore, spiny pocket mice can be selective about which plant species are consumed (Martínez-Gallardo and Sánchez-Cordero 1993), and need a constant food supply as they are sysceptible to rapid weight loss and can quickly become weak and die (Fleming 1977, Martínez-Gallardo and Sánchez-Cordero 1993). Thus, the ability of the intervening matrix to provide proper food resources can greatly affect the success of dispersal. Data on frogs and lizards in this area indicate that these communities are affected by fragmentation. Species richness was lower in all forest fragments combined compared to La Selva, and densities differed also; however, Bell and Donnelly (2006) concluded that a vast network of small forest patches may still be of conservation value in the Caribbean lowlands. The increased isolation of La Selva also has been hypothesized to have caused the decline of understory insectivorous birds (Sigel et al. 2006).

The sex ratio for adult spiny pocket mice did not differ from 1:1 for the entire dataset combined. Sex ratios can be altered by changes in the ecology or behavior of species. These changes can be associated with alteration of the environment (Dantas et al. 2009, Frankham

1995, Seger and Stubblefield 2002). Herein, we observed similar sex ratios in large fragments and small fragments. Fleming (1974) found male:female ratios to differ among two years at La Selva (0.88 and 0.30), but overall, found that the sex ratio did not differ from 1:1. Our results indicate that fragmentation is likely not having an effect on the sex ratios of spiny pocket mice.

Our reported mean mass for males and females for all of our sites combined is similar to those reported in La Selva previously (Fleming 1974). Mass between males and females differed, but we did not see sex-specific mass differences across large and small fragments. Thus, fragment size does not seem to have affected body condition of these mice.

This study represents the largest reported rodent trapping effort in terms of trap nights and areas sampled in the Caribbean lowlands of Costa Rica. The results indicate that rodent populations can be variable with relatively high abundances in some locations and low, or non-existent in smaller forest patches. Small and isolated patches appear to suffer from the most depauperate rodent communities, and have the lowest relative abundance of spiny pocket mice. Although these communities are difficult to study because of the low trap success and difficult terrain, they are still important components of the Caribbean lowland ecosystems, and more studies need to address these rodent populations that are of low-abundance in the Caribbean lowlands, and therefore, potentially more vulnerable to negative anthropogenic influences.

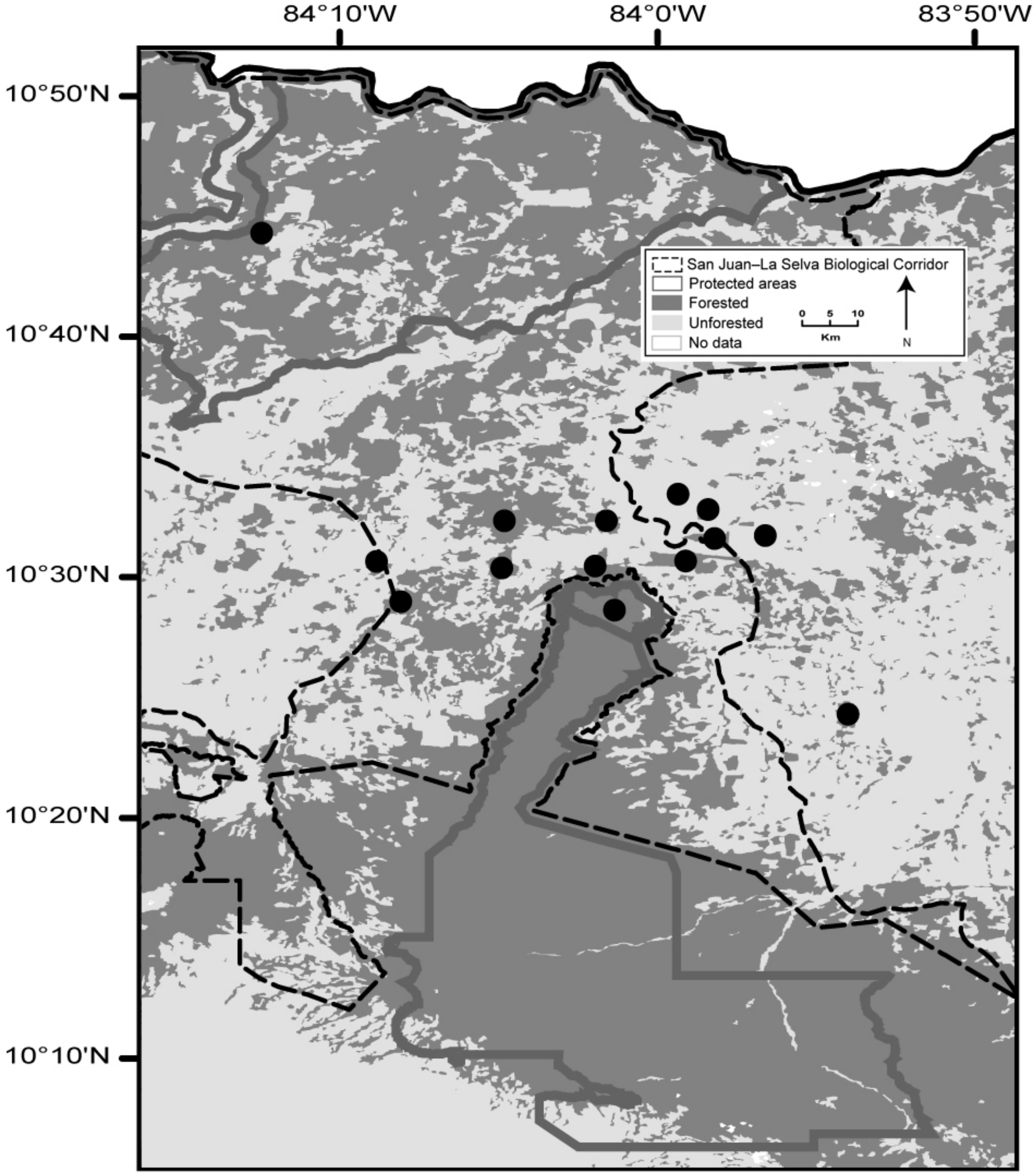

Figure 3.1—Fragments sampled in the Caribbean lowlands of Costa Rica. The site Berlin is omitted from this map.

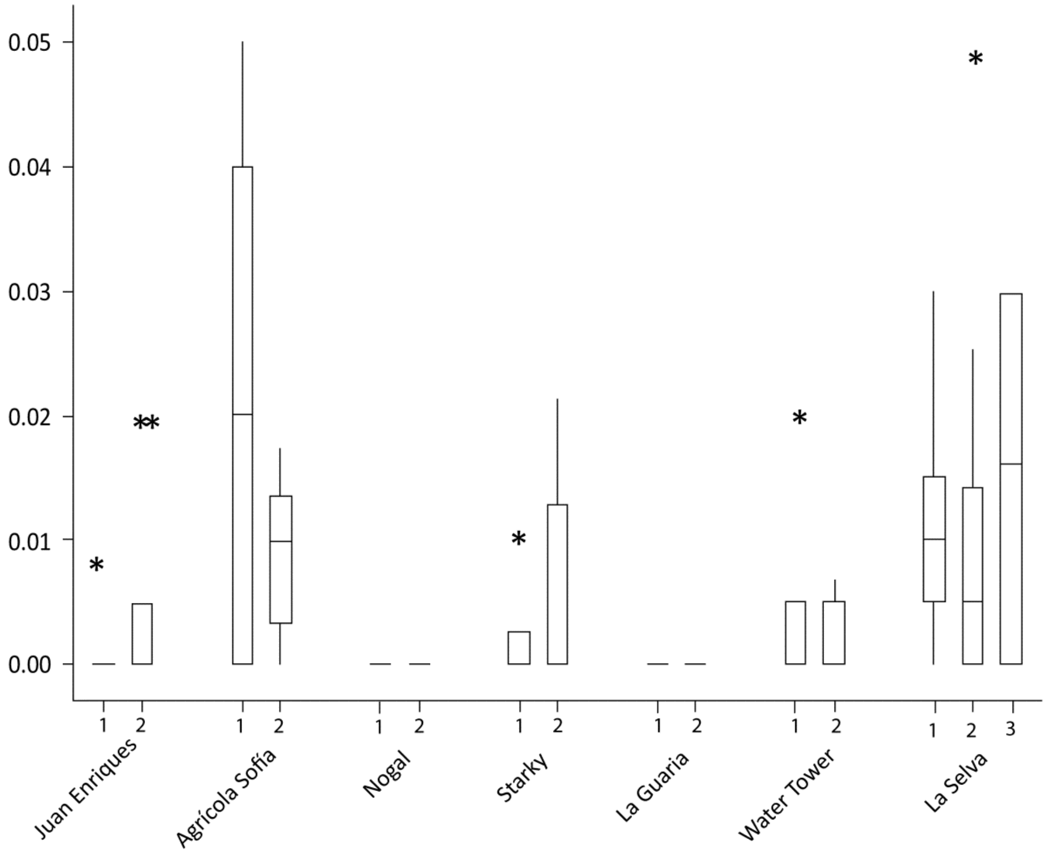

Figure 3.2—Boxplot showing nightly trap success for spiny pocket mice in sites that were sampled across multiple years. Middle line in box is the median with the outer edges of the box being Q1 and Q3. Outliers are indicated by *. Nogal and La Guaria had zero captures for all sampling periods. Mann–Whitney U tests for each site showed no significant differences across years (only years 1 and 2 were tested for La Selva as year 3 only had 3 data points).

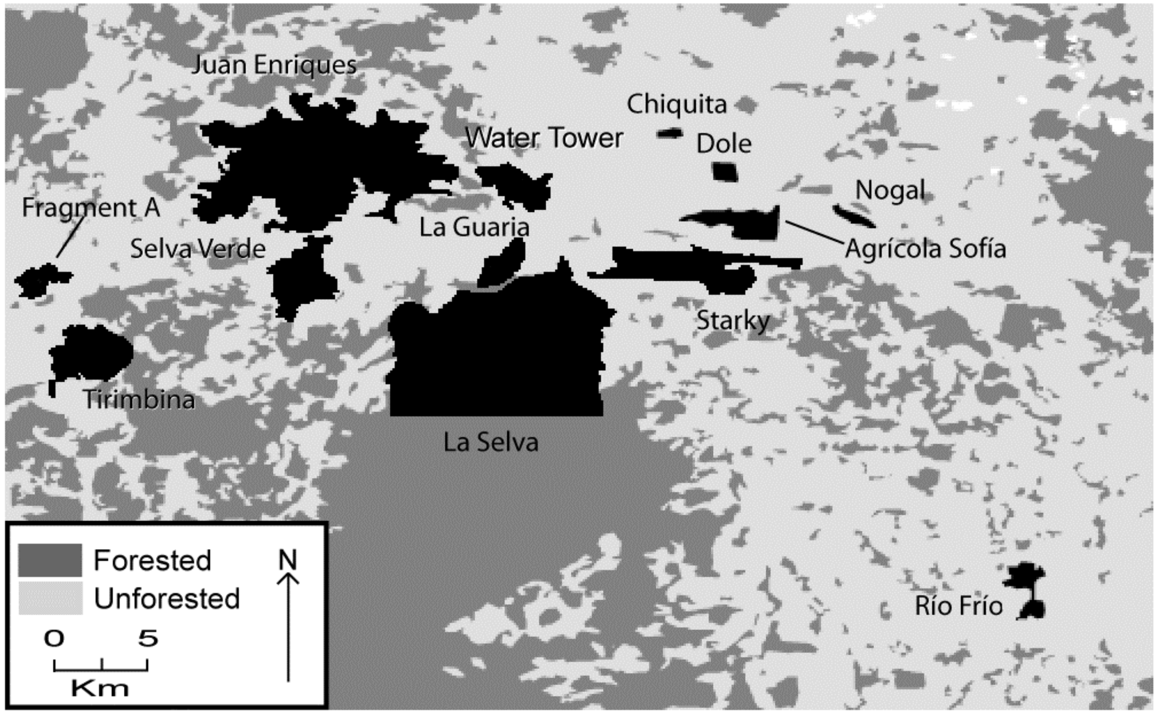

Figure 3.3–Zoomed in map of fragments sampled around La Selva Biological Station.

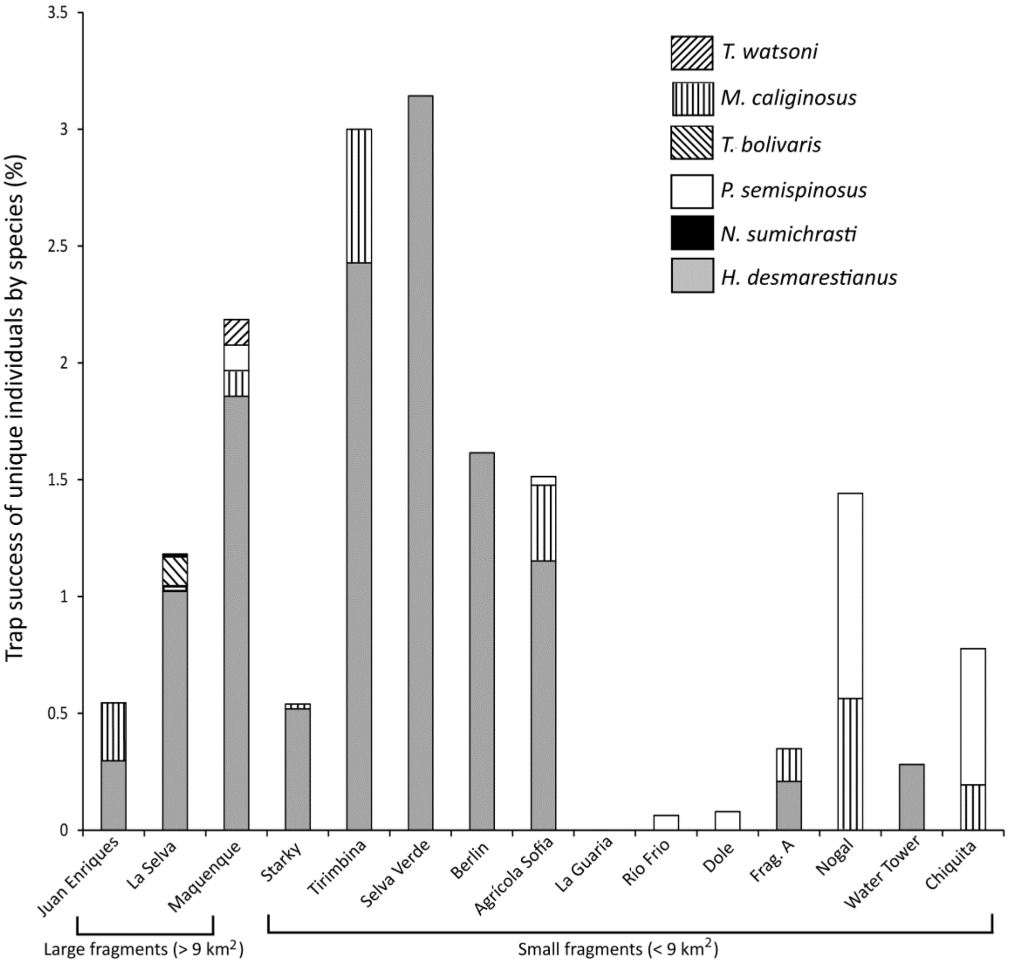

Figure 3.4—Unique individual trap success in each surveyed area by species. Sites are arranged in decreasing area.

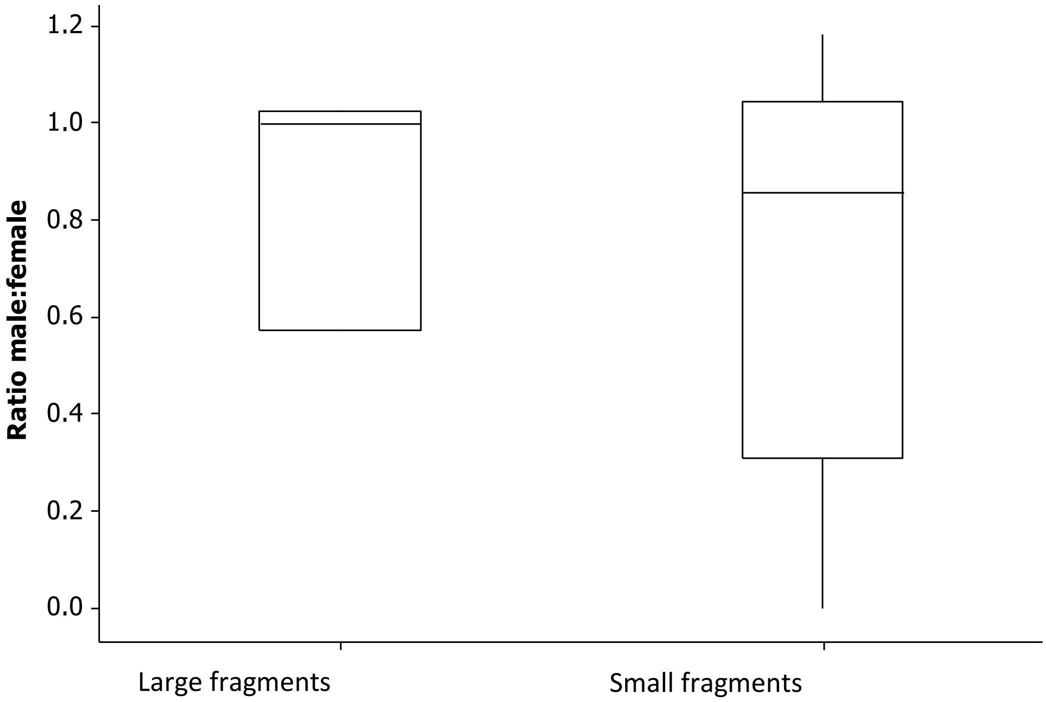

Figure 3.5—Boxplot of male:female ratios in large and small fragments. Middle line in box is the median with the outer edges of the box being Q1 and Q3. Lines beyond box represent upper and lower fence which is 1.5 × interquartile range.

Table 3.1—Physical characteristics of sampled fragments.

Site	Area (km^2)	Perimeter (km)	Max elev. (m)	Min elev. (m)	Latitude	Longitude
La Selva	14.41	20.7	146	22	10°25’47.90”N	84°00’55.15”W
Juan Enriques	17.3	38.3	190	46	10°27’20.46”N	84°04’01.70”W
Selva Verde	2.52	3.39	165	84	10°26’46.36”N	84°04’00.62”W
Tirimbina	3.86	8.95	224	149	10°24’45.58”N	84°07’02.55”W
Nogal	0.29	0.37	55	46	10°27’29.90”N	83°56’46.43”W
Agrícola Sofía	1.82	8.72	69	51	10°27’32.01”N	83°58’41.40”W
Maquenque	9.49	24.98	70	47	10°40’48.96”N	84°10’39.65”W
Starky	3.92	15.30	69	43	10°26’31.73”N	83°59’09.16”W
Chiquita	0.22	1.98	58	49	10°29’15.10”N	83°59’11.84”W
Water Tower	0.25	3.14	98	42	10°27’52.90”N	84°00’29.47”W
Frag. A	0.35	3.12	162	131	10°26’03.92”N	84°07’42.76”W
Dole	0.35	2.71	60	46	10°28’28.10”N	83°58’28.77”W
Río Frío	0.88	6.99	110	96	10°19’32.25”N	83°54’17.64”W
Berlin	2.14	6.69	280	210	10°07’59.73”N	83°36’18.38”W
La Guaria	1.14	6.25	67	52	10°26’34.24”N	84°01’27.71”W

Table 3.2—Trapping data for all sites and all years. Trap success is reported for all individuals, including recaptures, and for unique individuals. Trap success in parenthesis is for the spiny pocket mouse *Heteromys desmarestianus* only. La Selva sites are numbered by locality of trapping within the station.

Site	Year	Trap nights	Trap success	Trap success-unique individuals	Trapping method
Juan Enriques	2007	910	0.99% (0.22%)	0.88% (0.11%)	Grid and Trap lines
Selva Verde	2007	700	5.43% (5%)	3.71% (3.14%)	Grid
La Selva–1	2007	700	2% (2%)	1.43% (1.43%)	Grid
La Selva–2	2007	700	1% (0.71%)	0.86% (0.71%)	Grid
La Selva–3	2007	700	2% (2%)	1.14% (1.14%)	Grid
Tirimbina	2007	700	4.29% (3.57%)	2.71% (2.43%)	Grid
Nogal	2007	700	4.43% (0%)	3.29% (0%)	Grid
Agrícola Sofía	2007	700	6% (4.14 %)	3.43% (2.14%)	Grid
Maquenque	2007	915	3.06% (2.73%)	2.19% (1.86%)	Grid and Trap lines
La Selva–4	2008	545	1.10% (0.55%)	0.92% (0.37%)	Trap lines
La Selva–2	2008	1370	0.94% (0.72%)	0.79% (0.58%)	Trap lines
La Selva–1	2008	1625	1.12% (1.01%)	1.01% (0.88%)	Trap lines
La Selva–3	2008	1231	1.12% (0.86%)	0.95% (0.69%)	Trap lines
Juan Enriques	2008	3125	0.51% (0.42%)	0.45% (0.35%)	Trap lines
La Selva–5	2008	1117	2.06% (2.06%)	1.61% (1.61%)	Trap lines
Starky	2008	1188	0.26% (0.17%)	0.26% (0.17%)	Trap lines
Starky	2009	1249	1.29% (1.29%)	1% (1%)	Trap lines
Nogal	2009	751	0.11% (0%)	0.11% (0%)	Trap lines
Agrícola Sofía	2009	2076	1.16% (1.11%)	0.87% (0.82%)	Trap lines
Dole	2009	2076	0.08% (0%)	0.08% (0%)	Trap lines
La Guaria	2009	2782	0% (0%)	0% (0%)	Trap lines
Chiquita	2009	1029	0.78% (0%)	0.78% (0%)	Trap lines
Starky	2009	2240	0.40% (0.40%)	0.40% (0.40%)	Trap lines
Water Tower	2009	1955	0.46% (0.46%)	0.36% (0.36%)	Trap lines
Water tower	2010	2298	0.30% (0.30%)	0.22% (0.22%)	Trap lines
Río Frío	2010	1575	0.06% (0%)	0.06% (0%)	Trap lines
Frag A	2010	1434	0.42% (0.21%)	0.35% (0.21%)	Trap lines
La Guaria	2010	550	0% (0%)	0% (0%)	Trap lines
La Selva–5	2010	326	1.22% (1.22%)	1.22% (1.22%)	Trap lines
Berlin	2010	495	1.62% (1.62%)	1.41% (1.41%)	Trap lines

CHAPTER 4

REPRODUCTIVE STRATEGIES AND NATURAL HISTORY OF THE ARBOREAL NEOTROPICAL VESPER MOUSE, *NYCTOMYS SUMICHRASTI*

Abstract

The vesper mouse, *Nyctomys sumichrasti* (Rodentia: Cricetidae), a poorly known, arboreal, nocturnal, rodent found in Central America, has been considered rare, and limited information is available about its biology, especially reproduction. We obtained vesper mice from several sites in Costa Rica and prepared them as scientific specimens with standard external measurements and reproductive data recorded. We expanded our dataset by including specimens from museum collections. Vesper mice have 1:1 sex ratios throughout their range. They reproduce year-round and litters may occur in rapid succession. Testis size is positively correlated with body mass, but we could not determine onset of sperm production. The onset of reproduction for females, based on mass, is variable but most females are parous by 60 g. Litter size is small with a mode of 2 and embryos are not evenly distributed across the uterine horns. Vesper mice exhibit striking morphological differences in terms of tooth-wear and pelage patterns across their range. Much work is needed to fully appreciate *N. sumichrasti*, its role in tropical habitats, and its reproductive biology.

Introduction

The vesper mouse, *Nyctomys sumichrasti* (Saussure, 1860), is a poorly known, medium-sized cricetid rodent found from Jalisco and Veracruz, Mexico to central Panama, excluding the Yucatan Peninsula (Genoways et al. 2005, Hunt et al. 2004). Vesper mice are distinctive with an orange to tawny-brown dorsum, white underside, long whiskers, and a long, tufted tail, though there is morphological variation along its range. Vesper mice live in many habitats including evergreen, semi-deciduous, old secondary growth, and dry tropical forests (Fleming 1970, Reid 2009), and can be found from lowlands to elevations of 1,500–1,800 m (Timm and LaVal 2000, Timm et al. 1989). Historically, vesper mice have been treated as belonging to a single species, *N. sumichrasti*; however, recent studies suggest that more than one biological species may be involved (Corley et al. 2011, Timm and Genoways in prep.). Because vesper mice, along with the closely related Yucatan vesper mouse, *Otonyctomys hatti* Anthony, 1932, belong to a clade of closely related arboreal taxa, we herein will use the common name vesper mouse in discussing the members of this clade that are currently considered the widespread species *N. sumichrasti*.

Vesper mice are nocturnal, arboreal, and move along areas with dense trees and vegetation (Fleming 1970, Schnell et al. 2010). They feed on fruits, flowers, seeds, leaves, and insects (Genoways and Jones 1972, Reid 2009, Timm and LaVal 2000, Timm and Vriesendorp 2003) and use the same habitats in all seasons (Domínguez-Castellanos et al. 2007). On average, males travel longer distances than females (Schnell et al. 2010).

Vesper mice generally are considered rare or uncommon (Timm 1994, Timm and Vriesendorp 2003) with densities of 0.87–4.09/ha reported in Colima, Mexico (Schnell et al. 2010), but they are seemingly locally abundant in the Pacific lowlands of Nicaragua (Genoways and Jones 1972) and the Monteverde region of Costa Rica (Timm and Vriesendorp 2003). Abundance estimates may not be representative of true densities however, because they are difficult to see and infrequently caught (Ceballos 1990, Dalquest 1996, Fleming 1970, 1973). Vesper mice are hard to capture because traps must be placed above ground level, requiring special equipment, knowledge, and considerable effort; consequently, most aspects of the biology are poorly understood. Knowledge of reproduction is limited to a study of animals raised in captivity, inferences from a study in a Nicaraguan dry forest, incidental captures reported in small mammal surveys, and descriptions of the male reproductive organs (Arata

1964, Birkenholz and Wirtz 1965, Burt 1960, Fleming 1970, Genoways and Jones 1972, Hooper and Musser 1964, Sánchez-Hernández et al. 1999, Schnell et al. 2010). Data on reproduction and natural history are especially lacking for populations in the Caribbean lowland wet forests, which differ in patterns of seasonality and rainfall, potentially affecting reproductive strategies.

Basic knowledge on reproduction is critical for understanding how a species functions in its environment and in building accurate demographic and population growth models. Though *N. sumichrasti* may be more common than previously thought, its habitat has suffered considerable fragmentation and degradation (Peña et al. 2005, Sánchez-Azofeifa et al. 2001); thus, studies elucidating its ecology and reproduction are timely. Additionally, this arboreal mouse allows us to test predictions concerning the reproductive strategies of mammals that are highly mobile and agile in tropical environments, characteristics that can affect seasonality of reproduction, litter size, and embryo balance. Most vertebrates in the tropics, including a variety of mammals, show seasonal reproduction (Sasa et al. 2009, Stoner and Timm 2011), however based on the limited data available for *N. sumichrasti*, we predict year-round reproduction. Because this mouse is arboreal, has relatively large young, and may reproduce year-round, we expect litters to be small and evenly distributed across the uterine horns, given that these are characteristics associated with mammals that rely on speed and agility (Baird and Birney 1985, Birney and Baird 1985). The aim of this paper is to (1) determine sex ratios, (2) assess seasonality of reproduction, (3) test for a correlation between testis length and body mass, (4) determine the onset of female reproduction, (5) define litter size, (6) test for embryo balance between uterine horns, and (7) provide new information on the natural history and abundance of this poorly-known species.

Materials and methods

We obtained *N. sumichrasti* from several sites in Costa Rica, primarily in the northeastern Caribbean lowland tropical wet forests around Estación Biológica La Selva and Reserva Ecológica Bijagual. The 1600-ha La Selva reserve (10°25′52″ N, 84°00′12″ W) is owned and managed by the Organization for Tropical Studies and composed of primary forest, secondary forest, and abandoned pasture and plantations, with elevation ranging from 22 m to just over 140 m. La Selva receives ~ 4 m of rain annually, with a short dry season occurring February–April (McDade and Hartshorn 1994). Bijagual is a 290-ha private reserve (10°21′48″ N, 84°6′12″ W) comprised of 210 ha of selectively logged forest, with the remaining area being secondary growth and abandoned pasture. Mean annual rainfall at Bijagual is 5.5 m and elevation is 300–400 m above sea level (http://www.bijagual.org). Both reserves are in Heredia Province and connect to Costa Rica's Parque Nacional Braulio Carrillo.

Our complete dataset consists of specimens we prepared and other museum specimens. For the Caribbean lowland sample, reserve managers and private homeowners captured vesper mice that entered buildings from December 2005 to December 2009 (84 individuals). For each individual we recorded mass, using Pesola scales, and standard external measurements (total length, length of tail vertebrae, length of hind foot, and height of ear from notch) with a standard metric ruler. For females, we assessed (a) if they were nulliparous (defined as not lactating, no embryos, no enlarged mammary tissue, no open vaginal orifice, no enlarged uterus or placental scars); (b) number of embryos; (c) location of embryos (right or left uterine horn); (d) crown-to-rump length of embryos; and (e) size of mammae (visibly enlarged or not) and condition of the vaginal opening. Testis length and width were measured for males. All specimens were deposited at the University of Kansas Natural History Museum (KU), Lawrence or Museo Nacional de Costa Rica, San José. Our complete dataset (597 individuals) includes information on specimens from Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, and Panama, encompassing the entire range for this species. These were housed in the following institutions: American Museum of Natural History (AMNH), New York; Carnegie Museum of Natural History (CMNH), Pittsburgh; Field Museum of Natural History, Chicago (FMNH); Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM), Ciudad de México; Los Angeles County Museum (LACM), Los Angeles; Museo Nacional de Costa Rica (MNCR), San José; Museum of Vertebrate Zoology, Berkeley (MVZ); Royal Ontario Museum (ROM), Toronto; University of Kansas Natural History Museum (KU), Lawrence; and US National Museum (USNM), Washington, DC.

Sex ratios—We tested for deviations from a 1:1 sex ratio using a chi-square test for (1) all age classes (adults, subadults, and juveniles) pooled for individuals from the Caribbean lowlands of Costa Rica, and (2) all age classes and populations pooled for all countries. We did not test sex ratios by age classes because of difficulties in reliably assigning individuals to an age class based on tooth-wear patterns proposed by Genoways and Jones (1972). Although sampling biases can affect sex ratio analyses of a population, it should be reduced in this study due to our large dataset from museum specimens collected with a variety of techniques. Herein, we follow the same methodology in testing for sex ratio deviations as has been done for this species in the past (Genoways and Jones 1972, Schnell et al. 2010), and present the best estimates of sex ratios in this species to date.

Reproduction—We assessed seasonality of reproduction by tallying currently reproductive females (pregnant, lactating, or enlarged mammary tissue) by month for individuals from the Caribbean lowlands only, and for all possible specimens regardless of locality. A Pearson correlation analysis was performed with testis length and body mass. We scored all females we collected, regardless of locality, as reproductive or non-reproductive—females that were lactating, or had embryos, enlarged mammary tissue, an open vaginal orifice, an enlarged uterus, or placental/uterine scars were considered reproductive. We used a binary logistic regression to predict the probability of female reproductive state based on mass. Model fit was assessed using the Hosmer–Lemeshow test. All females with counts of visible embryos, regardless of locality or size of embryos, were used to determine litter size.

Embryo balance—We evaluated embryo balance in the uterine horns following the protocol outlined by Baird and Birney (1985). All pregnant females with 2 or more embryos, regardless of collection locality, were included in this analysis. Baird and Birney (1985) classified the embryo distribution for each female as balanced or unbalanced. To be considered balanced, an even-numbered litter would have to be split evenly between left and right uterine horns; however, an odd numbered litter is considered balanced if 1 horn had only 1 more embryo than the other (for example a litter size of 3 was considered balanced if the left horn had 1 embryo and the right had 2 embryos or vice versa).

Probabilities for every possible configuration for all litter sizes were determined using the binomial distribution with the probability of left and right being equal. For example, a litter size of 3, has 2 possible configurations, 3:0 or 2:1, with probabilities of 0.25 and 0.75, respectively. We then calculated a chi-square value for the observed distributions of the embryos (right or left uterine horn) for each litter size. Any litter size with an expected number fewer than 5 was pooled with an adjacent litter size. Chi-square values for all litter sizes were summed and compared to a chi-square distribution to test for significance. See Baird and Birney (1985) for a more detailed description of the method.

Statistical tests were run in MINITAB 14. This project was undertaken with the approval of the University of Kansas Institutional Animal Care and Use Committee. All animal handling protocols were in accordance with the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Results

Sex ratios—We examined 43 males and 41 females in all age classes from the Caribbean lowlands of Costa Rica. This ratio does not differ significantly from 1:1 ($\chi^2_1 = 0.048$, $P = 0.827$). Our dataset for all countries consists of 291 males and 306 females, totaling of 597 individuals. This male to female ratio of 1:1.05 does not significantly differ from 1:1 ($\chi^2_1 = 0.377$, $P = 0.539$).

Reproduction—Reproduction occurs year-round for both the Caribbean lowland population and for individuals across the geographic range. Parous and nulliparous females were found year-round for the Costa Rican Caribbean lowland population and for the entire dataset (Table 4.1). Male testis length ranged from 2–18 mm (mean = 9.97 mm, median = 11 mm, SD = 3.25). Male testis length was positively correlated with body mass ($r = 0.659$, $P < 0.001$, Fig. 4.1).

Females with greater mass were more likely to be reproductive. The binary logistic regression was found to be significant, with all coefficients in the model non-zero (log likelihood test, $G_1 = 43.884$, $P < 0.001$); goodness-of-fit tests showed no significant deviation from the model (Hosmer–Lemeshow $\chi^2_8 = 6.229$, $P = 0.622$). The equation estimating the probability of a female being reproductive is $P = e^{(-6.81+0.1669*M)}/(1+e^{(-6.81+0.1669*M)})$, where P is the probability of being reproductive and M is mass in grams. The estimated probability of a female being reproductively active begins to rise from 0 at ~20 g. At ~41 g the probability of a female being reproductive is 50%, which increases to nearly 100% at ~60 g (Fig. 4.2). We recognize that pregnant females can confound these results because of embryo weight, and for this reason we reran this analysis excluding pregnant females and found minor differences (e.g., 50% probability = 44 g). Here we report the analysis including pregnant females because the differences in the logistic regressions are inconsequential, and mass is regularly measured in the field and laboratory without knowledge of pregnancy status, and is therefore a more practical and useful tool.

Our lightest reproductive female weighed 32.4 g and was categorized as having an enlarged uterus with no visible embryos. The heaviest female weighed 87 g but had no associated reproductive data. Our heaviest reproductive female weighed 80 g with 1 embryo measuring 12 mm. The heaviest reproductive female that was not pregnant weighed 78 g. Our heaviest non-reproductive female weighed 56.6 g.

Out of 163 females with reproductive data, 24 were pregnant. The number of embryos varied from 1–4 (mean = 2.3, median and mode = 2, SD = 0.806). Crown–rump length varied from small embryos (2 mm) to more developed fetuses (32 mm) (weighted mean = 12.8 mm, SD = 8.03) (Table 4.2).

Embryo balance—Pregnant females with 2 or more embryos did not exhibit a balanced distribution within the uterine horns ($\chi^2_1 = 0.9$, $P = 0.66$) (Table 4.2).

Discussion

Sex ratios—The Caribbean lowland population did not differ from a 1:1 sex ratio for all age classes. Many of our specimens from Costa Rica's Caribbean lowlands were captured when they entered homes, therefore we mostly sampled individuals that were highly mobile or dispersing. These data suggest that both males and females are establishing new territories or dispersing at similar rates. Animals that were captured over a 48-month period at a single building ($n = 56$) ranged in mass from 20 to 80 g (mean = 46.7 g). This range in mass suggests that there is considerable movement of all size classes and ages. This 1:1 sex ratio is consistent with other studies in the dry forests of Nicaragua (Genoways and Jones 1972) and western Mexico (Schnell et al. 2010).

The sex ratio for all age classes and countries also did not differ from 1:1, which is likely representative of wild populations. Although collection biases can affect these analyses, we believe these biases to be reduced because museum specimens were collected using a variety of techniques including live traps, snap traps, incidental collection of dead animals, and collection with pistols.

We did not test sex ratios by age classes because of inherent difficulties in reliably assigning individuals to a class. Genoways and Jones (1972) classified individuals from western Nicaragua into 5 age classes based on tooth wear patterns. They subsequently collapsed these into juvenile, subadult, and adult. Following their protocol and using their specimens, we attempted to classify the individuals from the Caribbean lowlands to these categories. However, we were surprised to find that tooth wear patterns were quite different between the 2 regions; none of our individuals, including the heaviest and largest (> 60 g), could be classified older than wear category II, a young subadult. This difference in tooth wear patterns suggests that the diets in these 2 regions are quite different. In the Caribbean lowlands, the dry season is characterized by somewhat less rain than in the rainy season, but seasonality is not as severe as in the dry forests of the Pacific lowlands. This contrast in seasonality undoubtedly causes a difference in availability of food items. Therefore, tooth wear patterns do not provide a reliable way to characterize individuals into age classes across the geographic range of vesper mice. Age classes also are difficult to assign based on pelage. Juveniles show a grayer, softer coat, but it is difficult to establish a standard coat color for subadults and adults that is consistent across the entire range or even within a single population. Future studies comparing *N. sumichrasti* populations should take special precautions when using morphological characters to classify age classes, as tooth wear patterns and pelage are not the same. This may be true also for other species of tropical rodents.

Reproduction—Reproduction in *N. sumichrasti* occurs year-round throughout the range, including the Caribbean lowlands of Costa Rica (Table 4.1). These data are consistent with incidental captures in different habitats of pregnant or lactating females in different seasons (Fleming 1970, Genoways and Jones 1972, Sánchez-Hernández et al. 1999, Schnell et al. 2010). Even though the Caribbean lowlands do not exhibit drastic seasonal changes between the rainy and dry seasons, many vertebrates, including several mammals, exhibit seasonal reproduction, which may be affected by food availability (Sasa et al. 2009, Stoner and Timm 2011). Vesper mice are seemingly not affected in the same way in terms of reproduction.

Testis size increases with body mass (Fig. 4.1). Male reproduction was hard to assess based on testis size because of the difficulty in determining production of sperm without histological examination. In small mammals, testis size can adequately describe reproductive condition, and can be correlated with developmental stages, making it a reliable measure of male reproductive activity (Kenagy 1979). Even though we are unable to produce a binary logistic regression curve for male reproductive activity similar to our analysis for females, it would be interesting in future studies to determine if the onset of sperm production is as variable as is reproduction in females, and how the onset of sperm production is correlated to testis size.

The binary logistic regression suggests that reproduction in females may begin at 20 g, however the probability of a female being reproductive does not reach 50% until 41 g and close to 100% until 60 g (Fig. 4.2). Vesper mice in captivity grow quickly reaching 40 g by week 3 and 55 g by week 11 (Birkenholz and Wirtz 1965). There is considerable overlap in mass among non-reproductive and reproductive females; the lightest reproductive female weighed 32.4 g and the heaviest non-reproductive female weighed 56.6 g. This disparity in mass and reproductive state suggests that the start of reproduction may be highly variable among populations, individuals, and seasons. We present the binary logistic regression using mass instead of any other morphological character because mass is an easy and reliable measurement to take in the field and because body mass correlates to the probability of survival and reproduction of adult small mammals (Sauer and Slade 1985, Sauer and Slade 1987).

The fact that *N. sumichrasti* is tropical and arboreal may influence its reproductive strategies. Litter size for vesper mice is small (Table 4.2), which may be due to the ability of *N. sumichrasti* to reproduce year-round. Litter-size variation between species and geographic variation within species has been found to vary considerably in mammals, especially in rodents. Litter size for species found in the Neotropics varies from 1 in pacas (*Cuniculus paca* (Linnaeus, 1766)) to as many as 10–15 in cotton rats (*Sigmodon*). Hypotheses concerning litter size suggest that it should be greater, and the number of litters per year should be lower, in species that occur in geographic areas with shorter season length compared to more lower-latitude or lower-elevation populations (Spencer and Steinhoff 1968). Studies for various rodent species have documented litter size to increase with latitude and elevation (Birney et al. 1974, Bowdre 1971, Long 1973, Oswald and McClure 1985). Vesper mice reproduce year-round and can produce consecutive litters quickly. In captivity, gestation is 30–38 days and 1 female gave birth to 5 litters during a 7-month period (Birkenholz and Wirtz 1965). In Costa Rica's Caribbean lowlands, we captured 3 females accompanied by offspring while being simultaneously pregnant. One female seemingly had 2 sets of litters with her as the pups weighed 8 g, 8.5 g, 24 g, and 29 g, and she had 3 embryos measuring 5 mm. The second female had 3 young weighing 18 g, 19 g, and 20 g while pregnant with 3 embryos measuring 19 mm, while the third female had 2 young weighing 20.75 g and 19 g and was pregnant also with 3 embryos measuring 16 mm. Litter size for vesper mice is low, but they reproduce year-round, and likely in quick succession. These successive litters are interesting findings, given that few of our adult females were pregnant at the time of capture. Our data do not allow us to explore reasons why some females reproduce in rapid succession whereas others do not—perhaps after a series of rapid reproductive bouts there is a hiatus. In addition, these data suggest that vesper mice have postpartum or lactation estrus, resulting in the overlap of some litters (Gilbert 1984). Although we are unable to rigorously test for geographic variation and elevational variation in litter size for *N. sumichrasti* because of small sample sizes, our data suggest little to no variation geographically.

Vesper mice are highly arboreal which could affect litter size. Their movement has been described as a "series of short, rapid dashes, even when not unduly excited" (Birkenholz and Wirtz 1965:182). Small litter sizes may be advantageous given their need to be agile while moving on vines and trees. Members of this well-defined clade, the subfamily Tylomyinae—*Nyctomys*, *Tylomys*, *Ototylomys*, and *Otonyctomys*—and many other arboreal Neotropical rodents also have small litters ranging from 1–4 (Helm 1975, Itzá-Ortiz et al. 2011, Reid 2009). Unfortunately, little is known about the reproductive biology of the members of this clade, making it hard to compare litter size, seasonality of reproduction, and other life history traits that could provide insight into how reproductive strategies are similar for tropical, arboreal rodents.

Embryo balance—Mammals that have small litter sizes, have precocial young, and are reliant on fast, agile movements, for example pronghorn (*Antilocapra americana* (Ord, 1815)) and plains viscacha (*Lagostomus maximus* (Desmarest, 1817)), often balance their embryos across uterine horns (Baird and Birney 1985, Birney and Baird 1985). Given that vesper mice have small litter sizes and are arboreal, we tested for embryo balance and found that this species did not balance embryos more than would be expected by chance. Several factors could influence these results. The majority of cricetid rodents (7 of 9) tested for embryo balance by Baird and Birney (1985) did not exhibit embryo balance, which may indicate a phylogenetic pattern, however, the species included in their analysis are not arboreal or saltatory. Our study was unable to reject the null hypothesis that embryos are randomly distributed between the left and right uterine horns, but with only 15 pregnant females with 2 or more embryos and appropriate fieldnotes, the power of the analysis was low. Dependence on fast, dexterous movement to escape predators, young with relatively high birth weights, and small litter sizes are characteristics hypothesized to be correlated with increased selection for balanced distribution of embryos. Many of these characteristics are shared by vesper mice and their close relatives, making this clade an interesting group with which to test this hypothesis, especially because our data suggest that this may not be the case for *N. sumichrasti*.

Natural history—Vesper mice are regularly found entering human homes in the Caribbean lowlands, as well as at mid and high elevations in the Monteverde region of Costa Rica. Homes that are susceptible to invasion are typically surrounded by vegetation. Most homes from which we received *N. sumichrasti* have adjacent gardens, or are surrounded by introduced plants or early-stage second growth. In homes, vesper mice make nests with papers, clothing, foam mattresses, and oven and refrigerator insulation. However, they rarely consume human food, and infrequently damage granola, seeds, or cheese stored in kitchens, whereas all other species of native mice that invade houses (*Peromyscus nudipes* (J. A. Allen, 1891), *Reithrodontomys gracilis* J. A. Allen and Chapman, 1897, and *Tylomys watsoni* Thomas, 1899), as well as introduced *Rattus rattus* (Linnaeus, 1758) and *Mus musculus* Linnaeus, 1758, damage stored grains and grain products. However, all rodents, including *N. sumichrasti*, are especially attracted to chocolate. Vesper mice nibble novel objects, and one resident informed us that the mice frequently chewed on plastic soda caps and condoms. Homeowners report that vesper mice can be captured using peanut butter for bait.

On several occasions females were seen moving with immatures clinging to the teats. Dead immatures, sometimes found by researchers along trails at La Selva, have likely fallen while clinging to an active female or from the nest. An immature individual that had hair but had not opened its eyes was found along a trail at La Selva where a coati (*Nasua narica* Linnaeus, 1766) was seen earlier rummaging through leaf matter on a tree branch, likely where there was a vesper mouse nest.

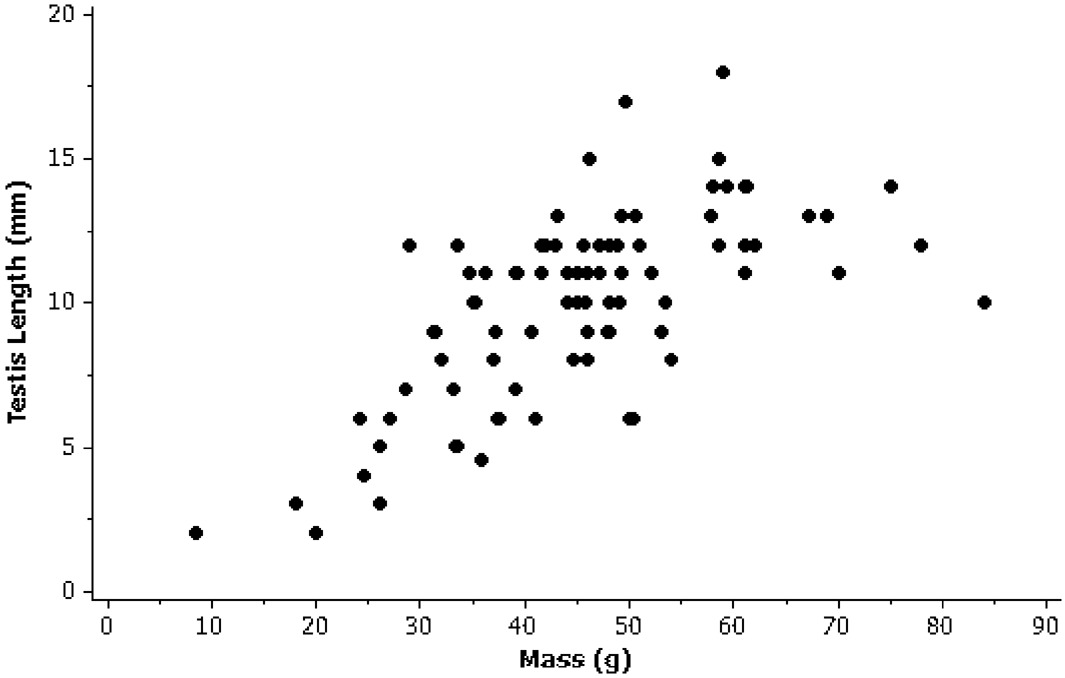

Figure 4.1—Testis length by mass. Males from all localities with testis length measurements were included (*n* = 87).

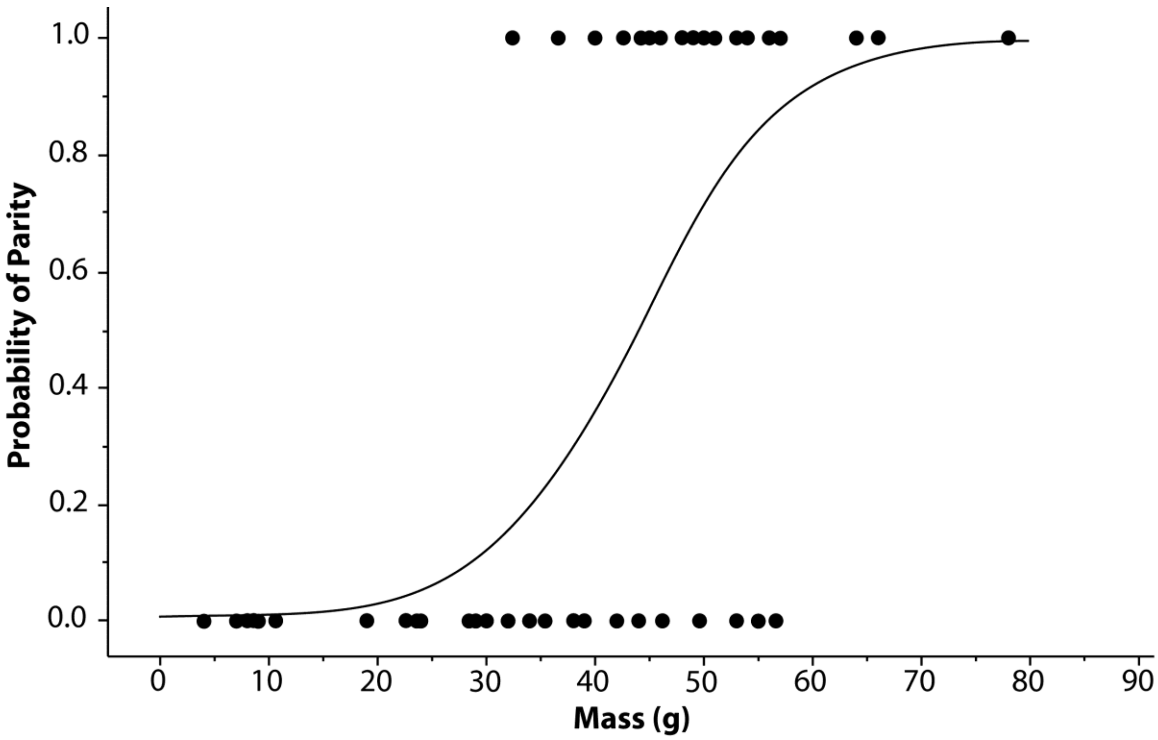

Figure 4.2—Binary logisitc regression for females with reproductive data from all localities (*n* = 72). Curve represents the probability of a female being reproductively active (parous) by weight. Parous females were individuals that were pregnant, lactating, and/or had enlarged mammary tissue or uterus.

Table 4.1—Reproductive status of female vesper mice from throughout the range collected by month. Reproductive category is broken down into individuals that were currently reproducing (pregnant = P, lactating = L, enlarged mammary tissue = EMT), and those that had signs of past reproduction (enlarged uterus = EU, uterine scars = US). Number reported in parenthesis is the number of individuals for each category for the Caribbean lowlands of Costa Rica only.

		Reproductive	
Month	Non-reproductive	P,L,EMT	EU, US
January	2 (2)	3 (2)	1 (0)
February	0	3 (2)	0
March	3 (0)	5 (1)	2 (0)
April	2 (1)	8 (2)	0
May	2 (2)	2 (1)	1 (0)
June	3 (3)	0	1 (1)
July	4 (3)	8 (4)	1 (1)
August	2 (1)	3 (0)	1 (0)
September	7 (4)	2 (1)	2 (1)
October	4 (1)	7 (2)	1 (0)
November	2	0	0
December	3 (1)	3 (1)	0

Table 4.2—Reproductive data for female vesper mice with embryos, for all countries. For each individual, the date of collection, total number of embryos (N), and number of embryos on the left (L) and right (R) horns of the uterus are shown. Crown–rump length (CR) of embryos is measured in mm.

Date	N	L	R	CR
10 Jul 1966	1	1	0	6
9 Feb 2008	1	N/A	N/A	12
10 Oct 2009	1	1	0	10
21 Apr 1927	2	N/A	N/A	20
26 Apr 1927	2	1	1	13
26 Apr 1927	2	2	0	8
13 Jul 1966	2	2	0	6
9 Aug 1967	2	1	1	32
18 Apr 1970	2	2	0	5
14 Oct 1992	2	N/A	N/A	14
12 Aug 1990	2	1	1	N/A
4 Feb 2008	2	1	1	15
24 Apr 2008	2	1	1	26
6 Jul 2009	2	0	2	3
13 Jul 2008	2	1	1	7
26 Oct 2008	2	1	1	L = 12; R = 10
22 Mar 1956	3	1	2	18
21 Mar 2006	3	1	2	7
15 Jul 2007	3	2	1	19
23 Jul 2007	3	1	2	16
5 Sept 2007	3	3	0	5
Unknown	3	N/A	N/A	25
19 May 1965	4	3	1	N/A
19 Aug 1967	4	2	2	2

CHAPTER 5

PHYLOGENETIC RELATIONSHIPS AMONG TWO GEOGRAPHIC REGIONS OF *HETEROMYS DESMARESTIANUS*: EVIDENCE OF A GENETICALLY DISTINCT POPULATION IN THE CARIBBEAN LOWLANDS OF COSTA RICA

Abstract

Phylogenetic studies provide important information about the evolutionary history and taxonomy of species, and can allow us to identify potential new species that are difficult to distinguish morphologically. The relationship among species in the genus *Heteromys* has been in flux as new species have been recently described, and new candidate species have been found in the *H. desmarestianus* group. Within this group, the species *H. desmarestianus* is widespread, from Mexico to Panama, but may actually be comprised of several cryptic species. One new potential species may be found in Costa Rica's Caribbean lowlands. Herein, we tested the phylogenetic relationship among individuals from Costa Rica's Caribbean lowlands to individuals from throughout the species' range. For our study we used *Cytb* sequences to test if individuals from the lowlands were genetically distinct from *H. desmarestianus.* We sequenced 116 individuals from the lowlands and incorporated 74 sequences available from GenBank from throughout the species' range. Our results strongly support individuals from Costa Rica's Caribbean lowlands being genetically distinct from *H. desmarestianus* individuals, including samples from elsewhere in Costa Rica. The results of our expansive sampling within the lowlands strongly suggest the presence of an unrecognized species, but because our data are limited to one locus, we are unable to definitively state this. Similar patterns of unrecognized rodent species in Costa Rica's Caribbean lowlands suggest that this area may hold hidden diversity, and further phylogenetic studies should make sure to incorporate samples from this area, as it may have a unique evolutionary history.

Introduction

Phylogenetic studies allow us to understand the relationship among species and identify potential species-level clades, which can have great impact on biodiversity studies (Agapow 2005, Chave et al. 2007). In particular, clear resolution of kinship among species or potential species-level clades is critical information needed to understand ecological communities, estimate species diversity at varying spatial scales, make conservation decisions, and understand the evolutionary history of taxa (Chave et al. 2007, Crandall et al. 2000, Crozier 1992, Faith 1992, Sinclair et al. 2005). Molecular methods are important for the study and delineation of species, particularly for those whose morphology provide no clear distinctions (Beheregaray and Caccone 2007, Bickford et al. 2007, Sinclair et al. 2005).

Due to the continual improvement of molecular methods and analyses, and broader sampling of natural populations, phylogenetic relationships are often in flux. One such example is the genus *Heteromys*, spiny pocket mice of the family Heteromyidae. In the early 1900's, Goldman (1911) recognized 13 species in the genus *Heteromys* and divided them into 2 subgenera—*Heteromys* and *Xylomys.* He further broke up the subgenus *Heteromys* into 2 species groups with the *H. desmarestianus* group comprised of 8 species, including *H. desmarestianus* described by Gray (1868). *Heteromys desmarestianus* has remained a valid species through several revisions of the genus (Hall 1981, Patton 2005, Rogers and González 2010, Rogers and Schmidly 1982, Williams et al. 1993), and several new species have been recognized in this species group (Anderson 2003, Anderson and Gutiérrez 2009, Anderson and Jarrín-V 2002, Anderson and Timm 2006). Recently, Rogers and González (2010) suggested four additional clades as candidate species within what is currently recognized as *H. desmarestianus*. The research we report here focused on one of these proposed candidate species, a clade that is located within the Caribbean lowlands of Costa Rica.

Heteromys desmarestianus, as currently defined, is common and widespread, ranging from southern Mexico to Colombia (Reid 2009). It is found in evergreen and semideciduous forests, from sea level to high elevation cloud forests (Reid 2009, Timm et al. 1989). *Heteromys desmarestianus* eat seeds, fruit, and insects, and can be the principal handlers of seeds, especially of palms (Brewer and Rejmánek 1999, Rosales Adame 1998). This species is important in Neotropical ecosystems; it acts as a seed predator, but can also increase seed dispersal and germination by scatterhoarding and caching seeds (Brewer 2001, Brewer and Rejmánek 1999, Klinger and Rejmánek 2010, Martínez-Gallardo and Sánchez-Cordero 1993, Sánchez-Cordero and Fleming 1993). Its ability to tolerate habitat fragmentation and degradation is unclear, as results from studies often vary (Klinger 2006, Sánchez-Cordero and Fleming 1993, Chapter 3), yet in the lowlands they appear to be negatively affected by fragmentation and thus may be of conservation concern (Chapter 3).

Heteromys desmarestianus is a difficult species to study in the Caribbean lowlands of Costa Rica, and consequently, is understudied (Chapter 3, Fleming 1974, Timm et al. 1989). Populations in this area are found at low densities, and fragmentation has further negative impacts on density (Chapter 3). As noted earlier, recent molecular evidence from mitochondrial and nuclear DNA of 3 individuals from the Caribbean lowlands (Rogers and González 2010) suggests that individuals found in these lowlands may actually represent a separate species from what is currently described as *H. desmarestianus*. The purpose of this study was to test, with the largest number of samples to date (116), if individuals from Costa Rica's Caribbean lowlands are genetically distinct from what is recognized today as *H. desmarestianus*.

Methods

We trapped mice in several locations throughout the Caribbean lowlands of Costa Rica from 2007–2010 (Fig. 5.1, Table 5.1). The Caribbean lowlands have similar ambient temperature throughout, but annual precipitation can vary from 2.4–4.8 m per year (McClearn et al. in press). Our localities (Table 5.1) ranged in elevation and size of forested area; our individuals from the highest elevation were from the Berlin property ranging from 210–280 m above sea level. Samples from Berlin also represented our southern-most sample. Our northern-most samples were from the Maquenque National Wildlife Refuge, close to the Costa Rica–Nicaragua border on the Río San Juan (Fig. 5.1).

We used Sherman traps (8 cm × 9 cm × 23 cm) (H. B. Sherman Traps, Inc., Tallahassee, FL) placed at ground level and baited with corn, oats, and mixed bird seed. Traps were checked daily, and when an individual was caught, a toe was removed with surgical scissors and immediately placed in 95% ethanol. All vials with tissue and ethanol were stored frozen within hours of collection. This project was undertaken with the approval of the University of Kansas Institutional Animal Care and Use Committee. All animal handling protocols were in accordance with the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Laboratory procedures—We utilized 116 samples in the laboratory from 10 sites in the Caribbean lowlands (Table 1). We soaked tissue in deionized water for 1 hr prior to beginning the digestion process. Standard digestion and DNA extraction were done following the protocol for mouse tails in Sambrook et al. (1989). The cytochrome-*b* (*Cytb*) gene was amplified in full using the primers 765 (forward) and 766 (reverse) (Bickham et al. 2004). Polymerase chain reaction (PCR) was performed using 50 μl reactions of the following reagents: 5 μl of 10x buffer, 5 μl of 10x salt, 5 μl of 10x solution of dNTP, 0.5 μl of Taq DNA polymerase, 5 μl of a 10x solution of each primer, 25 μl of deionized water, and 1–2 μl of DNA. Thermal cycle conditions consisted of initial heating at 94°C for 3 min, then 36 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 30 s, and extension at 70°C for 2.5 min. PCR products were purified using the QiAquick PCR purification kit (Qiagen, Valencia, CA) and were subsequently used in standard sequencing reactions using Big Dye version 3.0 (Applied Biosystems, Foster City, CA). Sequences were cleaned using Sephadex spin columns and were analyzed on an ABI 3100 automated genetic analyzer (Applied Biosystems, Forster City, CA). Sequence data were manually aligned using Sequencher v. 4.9 (Gene Codes Corporation, Ann Arbor, MI). We used the complete *Cytb* gene (1140 bp), and all flanking regions were discarded prior to phylogenetic analysis.

To expand our dataset, we used *Cytb* sequences of *H. desmarestianus* available from GenBank (Benson et al. 2013). We incorporated 74 sequences that represented samples from the species' range, and used *H. nelsoni* and two sequences of *H. australis* and *H. anomalus* as outgroups (Appendix 1). We aligned all sequences with Muscle v.3.8.31 (Edgar 2004) implemented in Jalview 2.8 (Waterhouse et al. 2009).

Phylogenetic analysis—Phylogenetic relationships were obtained by performing a maximum likelihood analysis. We estimated models of molecular evolution using jModelTest v.2.1.1 with the corrected Akaike information criterion test (Darriba et al. 2012, Guindon and Gascuel 2003). We used GARLI v. 2.0 (Zwickl 2006) for maximum likelihood analyses, using 2 independent search runs, with a maximum of 5 million generations each. We calculated support values using bootstrap with 500 replications in GARLI, and visualized and edited results with FigTree v.1.4 (Rambaut 2007).

Results

The aligned data set comprises of 1142 characters of which 738 characters were constant, 335 characters were parsimony-informative, and 69 variable characters were parsimony-uninformative. The model of DNA substitution, inferred from jModeltest 2.1.1 AIC, is TIM2+I+G.

The ML tree topology (Fig. 5.2) showed two highly supported branches for all *H. desmarestianus* individuals. One branch included all samples from Costa Rica's Caribbean lowlands and had very strong (99%) bootstrap support. The other branch included all of the *H. desmarestianus* GenBank samples obtained from Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, and Nicaragua and also had strong bootstrap support (83%). Within the branch that represented the samples from Costa Rica's Caribbean lowlands (not shown in Fig. 5.2), the individuals from two sites, Berlin and Maquenque, formed clades supported by strong bootstrap support. However, there were only three individuals sampled from Berlin, and two individuals from the eight sampled in Maquenque were placed elsewhere within the tree. Therefore, the nonexclusive nature of the branching pattern does not allow us to discern any lower level population patterns from these data.

Discussion

The results of this study, based on the mitochondrial marker *Cytb*, support the hypothesis that what is currently called *H. desmarestianus* in the Caribbean lowlands of Costa Rica is an unrecognized species (Rogers and González 2010). Many phylogenetic studies for animals have employed single mitochondrial DNA genes, particularly *Cytb*, to study taxonomic relationships (Farias et al. 2001, García-Moreno et al. 1999, Hackett 1996, Irwin et al. 1991) because the structure and function of the *Cytb* protein product is well understood, and the gene itself contains both conservative and more variable regions (Esposti et al. 1993). Our results are consistent with Rogers and González (2010), who used both *Cytb* and nuclear data, and identified 3 individuals from Costa Rica's Caribbean lowlands as a candidate species.

Although useful to characterize species that are difficult to establish based on morphological data, DNA sequence data do have limitations, particularly when a single marker is used (Farias et al. 2001, Rogers and González 2010). Now that we have provided extensive sampling of individuals from Costa Rica's Caribbean lowlands we recommend that future studies focus on sequencing more nuclear and mitochondrial markers from fewer individuals, and concentrate on determining morphological characters that could be used to identify these species in the field.

The family Heteromyidae originated on the North America continent (Schmidly et al. 1993, Wood 1935), and fossil remains for the subfamily Heteromyianae are known from the Pliocene, Pleistocene, and Holocene (Rogers 1990). Rogers (1990) estimated that the major groups within this subfamily diverged ~ 12–13 mya, yet the historical events that produced the *H. desmarestianus* group are largely unknown. The geologic history of the Caribbean, and Central and South America has been a contentious topic (Keigwin 1978, Kirby and MacFadden 2005, Malfait and Dinkelman 1972, Montes et al. 2012, Savage 1982), but it is thought that islands of volcanic origin between Central and South America may have allowed faunal exchanges from the late Cretaceous to the early Paleocene (Guyer and Savage 1992, Rogers 1990, Savage 1982). The time of the emergence of a permanent Panamanian land bridge is disputed, and estimates range from 2–7 mya (Marshall et al. 1982, Montes et al. 2012, Schmidly et al. 1993). Because of the widespread distribution pattern of the *H. desmarestianus* group, a hypothesis similar to the one suggested for other rodent groups (Baskin 1978, Patterson and Pasqual 1972, Rogers 1990, Simpson 1950, Simpson 1980) has been proposed for this clade. It is thought that considerable radiation occurred in the Miocene and Pliocene throughout Central America, with a subsequent entry to South America via the Panamanian land bridge (Rogers 1990, Schmidly et al. 1993). We believe that our results, in conjunction with future studies that aim to identify potential new species in the *H. desmarestianus* group, and the relationships between these species, will allow for a greater understanding of the historical events leading to the derivation of this group.

Our results show a clear geographic pattern; individuals currently considered *H. desmarestianus* in Costa Rica's Caribbean lowlands are genetically distinct from individuals found elsewhere in the Neotropics, including other areas in Costa Rica (Fig. 5.2). Costa Rica is only ~ 51,000 km^2, yet its variable topography and climate can result in diverse habitats with unique flora and fauna (Janzen 1983, Kappelle in press). Currently four main mountain ranges divide the country into the Pacific and Caribbean sides. These mountain ranges span southeast to northwest, and are of diverse ages and origins (Anderson and Timm 2006). Extending from western Panama to northern Costa Rica, the Cordillera de Talamanca, Cordillera Central, and Cordillera de Tilarán form an expansive mountain range with peak elevations of over 3000 m, 2500 m, and 2000 m, respectively. The Cordillera de Guanacaste is the northernmost range in Costa Rica, and is comprised of several isolated volcanoes, with passes of ~ 500–700 m in elevation that connect the Pacific and Caribbean sides (Anderson and Timm 2006). The historical and current topography of these mountain ranges probably shaped the diversification and speciation patterns observable today. Our results show a broad distribution of this distinct species within the Caribbean lowlands of Costa Rica, yet individuals from higher elevations on these mountain ranges are genetically distinct. Our northern-most specimens are from the Costa Rica–Nicaraguan border, while our southern-most specimens are ~ 86 km southeast of there. Unfortunately, little is known about *H. desmarestianus* in the lowlands of Nicaragua and southern Costa Rica, and we are unable to demarcate northern and southern boundaries for this potential new species. In terms of elevation, our specimens came from forests that ranged in elevation from ~ 22–280 m. In our analysis we included a single GenBank sequence from Cerro Honduras in Parque Nacional Braulio Carrillo. The park, along with privately owned reserves and biological stations, is part of a continuously forested transect that expands from the lowlands at La Selva Biological Station and reaches elevations > 2700 m. Although we do not have specific data on the elevation from which this particular specimen came, our results do show that this higher elevation specimen is in the clade with the other *H. desmarestianus* specimens from throughout Central America and does not group with our samples from the lowlands, including specimens from the nearby La Selva Biological Station. While our results indicate that the two specimen groups are genetically different, we are unable to delineate limits of their elevational range, and we do not know if there are any potential areas of overlap or hybridization.

The rodent communities of Costa Rica's Caribbean lowlands have been vastly understudied, in part, because of low densities resulting in low trap success (Chapter 3). Consequently, the lack of data and specimens has hindered our understanding of the basic phylogenetic relationships and biogeographic patterns of species in the area. Indeed, other widespread rodent species have been found to hold similar patterns reported herein, where individuals from Costa Rica's Caribbean lowlands are genetically distinct species that are currently unrecognized (Timm unpublished data). These data suggest that there may be hidden diversity in the lowlands, and that more phylogenetic studies should include samples from the lowlands to identify potential biogeographic patterns for rodents in the Neotropics. This information is necessary not only to understand species relationships, but also to have a grasp on the patterns and levels of diversity for the area, and make large-scale conservation decisions based on this information.

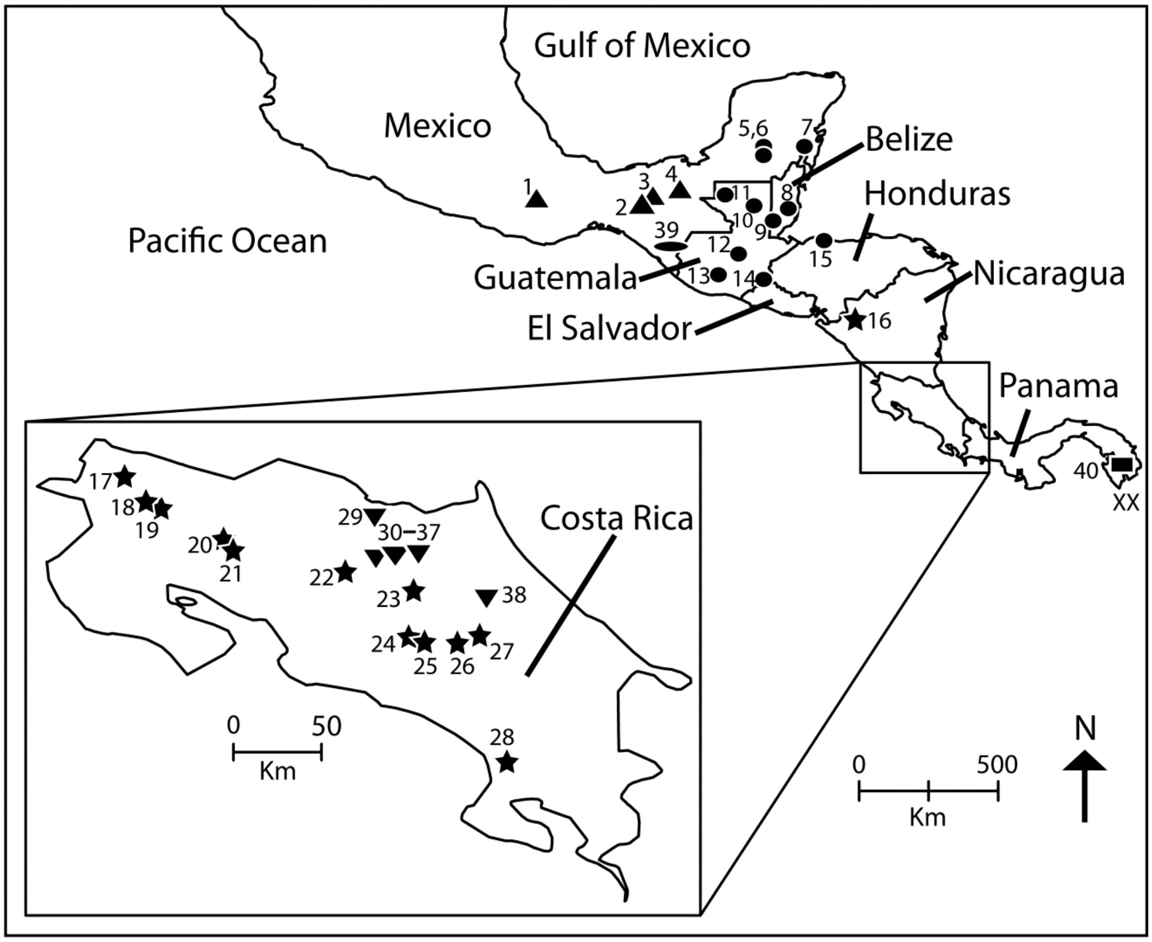

Figure 5.1—Map of localities for all specimens used in the study. Localities 29–38 represent specimens from Costa Rica's Caribbean lowlands. Symbols are coded with the results from maximum likelihood tree (Fig. 5.2). *H. anomalus* from Venezuela not depicted herein. Specific data regarding localities can be obtained from Appendix 1.

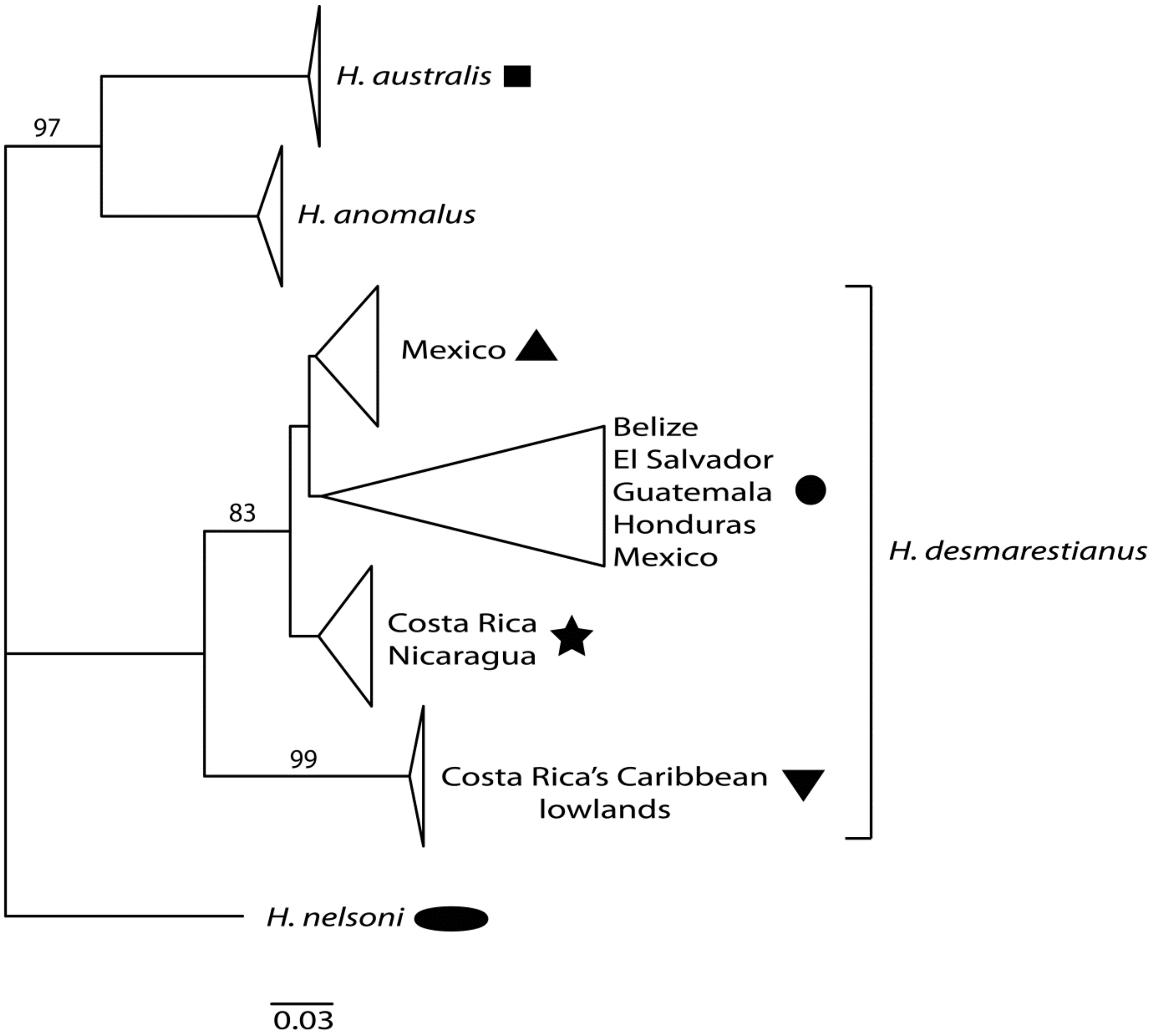

Figure 5.2—Collapsed maximum likelihood tree results with bootstrap values. Results strongly support that individuals from Costa Rica's Caribbean lowlands are likely a distinct, currently unrecognized species. Symbols in tree are used in Fig. 1 to show the geographic range of samples and particular localities.

Table 5.1—Sites and physical characteristics of areas sampled in Costa Rica's Caribbean lowlands. Locality numbers refer to numbers from figure 5.1.

Site (locality)	Area (km^2)	Perimeter (km)	Max elevation (m)	Min elevation (m)	Latitude	Longitude
La Selva (32)	14.41	20.7	146	22	10°25'47.90"N	84°00'55.15"W
Juan Enriques (31)	17.3	38.3	189.59	45.72	10°27'20.46"N	84°04'01.70"W
Selva Verde (30)	2.52	3.39	164.59	84.43	10°26'46.36"N	84°04'00.62"W
Tirimbina (33)	3.86	8.95	224.03	149.35	10°24'45.58"N	84°07'02.55"W
Agrícola Sofía (35)	1.82	8.72	68.58	51.21	10°27'32.01"N	83°58'41.40"W
Maquenque (29)	9.49	24.98	70.1	47	10°40'48.96"N	84°10'39.65"W
Starky (36)	3.92	15.30	69	43	10°26'31.73"N	83°59'09.16"W
Water Tower (34)	0.25	3.14	98	42	10°27'52.90"N	84°00'29.47"W
Frag. A (37)	0.35	3.12	162	131	10°26'03.92"N	84°07'42.76"W
Berlin (38)	2.14	6.69	280	210	10°07'59.73"N	83°36'18.38"W

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Appendix 1. Localities and specimen information for all samples utilized in the study. Map numbers correspond to numbers on Fig. 1. Data for specimens not from the Caribbean lowlands of Costa Rica were obtained from GenBank and the published papers associated with the GenBank accession numbers.

Map	Species	Specimen information	GenBank Accession number	Locality	Country
N/A	*H. anomalus*	CM 78170 = MDE 2087 = AK 3468	GU646919	Miranda, 25 km N Altagracia de Orituco, 500 m	Venezuela
N/A	*H. anomalus*	CM 78168 = MDE 2034 = AK3437	GU646924	Sucre, 40 km NW Caripito, 250 m	Venezuela
40a	*H. australis*	LSUMZ 35452 = MSH 1187 = TK 22565	GU646926	Darién, approximately 6 km NW Cana, E. slope Cerro Pirre, 1,200 m	Panama
40b	*H. australis*	ROM 104356 = F38215	GU646927	Darién, Cerro Pirre, Parque Nacional Darién	Panama
8a	*H. desmarestianus*	CM 91988 = AK7663	GU646929	Stann Creek District, 3.4 km WNW Quam Bank, Cockscomb Basin	Belize
8b	*H. desmarestianus*	CM91980 = AK7688	GU646930	Stann Creek District, 6.8 km WNW Quam Bank, Cockscomb Basin	Belize
8c	*H. desmarestianus*	CM 91951 = AK 7665	GU646932	Stann Creek District, 7.7 km WNW Quam Bank, Cockscomb Basin	Belize
9a	*H. desmarestianus*	CM 91991 = AK 7540	GU646933	Toledo District, 1.0 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9b	*H. desmarestianus*	CM 91989 = AK 7555	GU646934	Toledo District, 2.4 km NNW Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9c	*H. desmarestianus*	CM 91993 = AK 7588	GU646935	Toledo District; 2.1 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9c	*H. desmarestianus*	CM 91994 = AK 7586	GU646936	Toledo District; 2.1 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9c	*H. desmarestianus*	CM 91995 = AK 7589	GU646937	Toledo District; 2.1 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
18	*H. desmarestianus*	KU 158615 = MK 00-112	DQ450094	Guanacaste, Area de Conservación Guanacaste, approximately 20 km NNE Liberia, Pailas, Sendero Pailas, near Rio Colorado, 800 m	Costa Rica

17	*H. desmarestianus*	KU 158508 = MK 99-088	DQ450095	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla, Sendero Orosilito	Costa Rica
17	*H. desmarestianus*	KU 158509 = MK 99-090	DQ450096	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla, Sendero Orosilito	Costa Rica
17	*H. desmarestianus*	KU 158512 = MK 99-093	DQ450097	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla	Costa Rica
17	*H. desmarestianus*	KU 158513 = MK 99-094	DQ450098	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla	Costa Rica
17	*H. desmarestianus*	KU 158514 = MK 99-102	DQ450099	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla, Sendero Carica	Costa Rica
22	*H. desmarestianus*	ROM 113310 = F 48617	GU646938	Alajuela; 10 km E of Sucre, Parque Nacional, Juan Costro Blanco	Costa Rica
22	*H. desmarestianus*	ROM 113311 = F 48618	GU646939	Alajuela; 10 km E of Sucre, Parque Nacional, Juan Costro Blanco	Costa Rica
24	*H. desmarestianus*	ROM 113130 = F 48436	GU646940	Cartago, Iztaru, Cerros de la Carpintera	Costa Rica
24	*H. desmarestianus*	ROM 113131 = F 48437	GU646941	Cartago, Iztaru, Cerros de la Carpintera	Costa Rica
27	*H. desmarestianus*	MVZ 164823 = DSR 2153	GU646942	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164823 = DSR 2154	GU646943	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164825 = DSR 2166	GU646944	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164826 = DSR 2167	GU646945	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164827 = DSR 2246	GU646946	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
26	*H. desmarestianus*	ROM 97324 = FAR 111	GU646947	Cartago, 4 km SE of Turrialba by road, Catie, 600 m	Costa Rica
26	*H. desmarestianus*	ROM 97325 = FAR 112	GU646948	Cartago, 4 km SE of Turrialba by road, Catie, 600 m	Costa Rica
20	*H. desmarestianus*	MVZ 164828 = DSR 2123	GU646949	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164829 = DSR 2124	GU646950	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica

20	*H. desmarestianus*	MVZ 164831 = DSR 2134	GU646952	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164833 = DSR 2124	GU646953	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164835 = DSR 2143	GU646954	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
21	*H. desmarestianus*	MVZ 164839 = DSR 2121	GU646955	Guanacaste: 5.0 km NE (by road) Tilarán, 675 m	Costa Rica
21	*H. desmarestianus*	MVZ 164840 = DSR 2122	GU646956	Guanacaste: 5.0 km NE (by road) Tilarán, 675 m	Costa Rica
19	*H. desmarestianus*	ROM 113244 = F 48551	GU646957	Guanacaste: Volcán Santa Maria	Costa Rica
19	*H. desmarestianus*	ROM 113245 = F 48552	GU646958	Guanacaste: Volcán Santa Maria	Costa Rica
28	*H. desmarestianus*	LSUMZ 28354 = MSH 1260	GU646959	Puntarenas, 1 km N, 5 km W Palmar Norte, 33 m	Costa Rica
25	*H. desmarestianus*	BYU 15197 = EA 21	GU646960	San José, Bajo de Iglesia, SW Volcán Irazu, Cascajal de Coronado	Costa Rica
25	*H. desmarestianus*	BYU 15198 = EA 22	GU646961	San José, Bajo de Iglesia, SW Volcán Irazu, Cascajal de Coronado	Costa Rica
23	*H. desmarestianus*	BYU 15195 = EA 78	GU646962	San José, Parque Nacional Braulio Carillo, Moravia, Cerro Honduras	Costa Rica
23	*H. desmarestianus*	BYU 15196 = EA 79	GU646963	San José, Parque Nacional Braulio Carillo, Moravia, Cerro Honduras	Costa Rica
29	*H. desmarestianus*			Alajuela: Maquenque, 10°40′48.96″N, 84°10′39.65″W	Costa Rica
29	*H. desmarestianus*			Alajuela: Maquenque, 10°40′48.96″N, 84°10′39.65″W	Costa Rica
29	*H. desmarestianus*			Alajuela: Maquenque, 10°40′48.96″N, 84°10′39.65″W	Costa Rica
29	*H. desmarestianus*			Alajuela: Maquenque, 10°40′48.96″N, 84°10′39.65″W	Costa Rica
29	*H. desmarestianus*			Alajuela: Maquenque, 10°40′48.96″N, 84°10′39.65″W	Costa Rica
29	*H. desmarestianus*			Alajuela: Maquenque, 10°40′48.96″N, 84°10′39.65″W	Costa Rica
29	*H. desmarestianus*			Alajuela: Maquenque, 10°40′48.96″N, 84°10′39.65″W	Costa Rica
29	*H. desmarestianus*			Alajuela: Maquenque, 10°40′48.96″N, 84°10′39.65″W	Costa Rica
30	*H. desmarestianus*			Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*			Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica

30	*H. desmarestianus*			Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*			Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*			Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*			Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*			Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*			Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*			Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
31	*H. desmarestianus*			Heredia: Juan Enriques, 10°27′20.46″N, 84°04′01.70″W	Costa Rica
31	*H. desmarestianus*			Heredia: Juan Enriques, 10°27′20.46″N, 84°04′01.70″W	Costa Rica
31	*H. desmarestianus*			Heredia: Juan Enriques, 10°27′20.46″N, 84°04′01.70″W	Costa Rica
31	*H. desmarestianus*			Heredia: Juan Enriques, 10°27′20.46″N, 84°04′01.70″W	Costa Rica
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32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
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32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
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32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
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32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
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32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*			Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
33	*H. desmarestianus*			Heredia: Tirimbina, 10°24′45.58″N, 84°07′02.55″W	Costa Rica
33	*H. desmarestianus*			Heredia: Tirimbina, 10°24′45.58″N, 84°07′02.55″W	Costa Rica
33	*H. desmarestianus*			Heredia: Tirimbina, 10°24′45.58″N, 84°07′02.55″W	Costa Rica
33	*H. desmarestianus*			Heredia: Tirimbina, 10°24′45.58″N, 84°07′02.55″W	Costa Rica
33	*H. desmarestianus*			Heredia: Tirimbina, 10°24′45.58″N, 84°07′02.55″W	Costa Rica

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33	*H. desmarestianus*			Heredia: Tirimbina, 10°24′45.58″N, 84°07′02.55″W	Costa Rica
38	*H. desmarestianus*			Limon Province: Berlin, 10°07′59.73″N, 83°36′18.38″W	Costa Rica
38	*H. desmarestianus*			Limon Province: Berlin, 10°07′59.73″N, 83°36′18.38″W	Costa Rica
38	*H. desmarestianus*			Limon Province: Berlin, 10°07′59.73″N, 83°36′18.38″W	Costa Rica
34	*H. desmarestianus*			Heredia: Water Tower, 10°27′52.90″N, 84°00′29.47″W	Costa Rica
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35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
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35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
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35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
35	*H. desmarestianus*			Heredia: Agrícola Sofía, 10°27′32.01″N, 83°58′41.40″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica

36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
36	*H. desmarestianus*			Heredia: Starky, 10°26′31.73″N, 83°59′09.16″W	Costa Rica
37	*H. desmarestianus*			Heredia: 10°26′03.92″N, 84°07′42.76″W	Costa Rica
37	*H. desmarestianus*			Heredia: 10°26′03.92″N, 84°07′42.76″W	Costa Rica
14	*H. desmarestianus*	ROM 101369 = F 35547	GU646964	Santa Ana, Parque Nacional Montecristi, Bosque Nebuloso, 2,200 m	El Salvador
14	*H. desmarestianus*	ROM 101389 = F 35567	GU646965	Santa Ana, Parque Nacional Montecristi, Bosque Nebuloso, 2,200 m	El Salvador
11	*H. desmarestianus*	LVT 5499	AY926358	Tikal, El Peten	Guatemala
12	*H. desmarestianus*	ROM 98405 = FN 31394	GU646966	Baja Verapaz: 5 km E of Puruhla, 1,550 m	Guatemala
12	*H. desmarestianus*	ROM 98406 = FN 31395	GU646967	Baja Verapaz: 5 km E of Puruhla, 1,550 m	Guatemala
12	*H. desmarestianus*	FN 31402	GU646968	Baja Verapaz: 5 km E of Puruhla, 1,550 m	Guatemala
10a	*H. desmarestianus*	ROM 99603 = FN 32272	GU646969	El Peten: Biotope, Cerro Cahui, El Remate	Guatemala
10a	*H. desmarestianus*	ROM 99604 = FN 32273	GU646970	El Peten: Biotope, Cerro Cahui, El Remate	Guatemala
10b	*H. desmarestianus*	ROM 99469 = FN 32318	GU646971	El Peten: Campo los Guacamayos, Biotopo Laguna del Tigre, 40 km N El Naranjo	Guatemala
11	*H. desmarestianus*	ROM 99292 = FN 31842	GU646973	El Peten, Tikal	Guatemala
11	*H. desmarestianus*	ROM 99293 = FN 31843	GU646974	El Peten, Tikal	Guatemala

13	*H. desmarestianus*	ROM 98266 = FN 31252	GU646975	Sacatepequez, 5 km W San Miguel Duanas, 1,765 m	Guatemala
13	*H. desmarestianus*	ROM 98265 = FN 31254	GU646976	Sacatepequez, 5 km W San Miguel Duanas, 1,765 m	Guatemala
15	*H. desmarestianus*	TCWC 52259 = BEL 865 = AK 9696	DQ168466	Atlántida, Lancetilla	Honduras
1a	*H. desmarestianus*	MVZ 161229 = DSR 1685	DQ168467	Oaxaca; Distrito Ixtlán, Vista Hermosa, 1,000 m	Mexico
5	*H. desmarestianus*	ROM 97050 = FN 30853	GU646977	Campeche, 10 km N El Refugio	Mexico
5	*H. desmarestianus*	ROM 97051 = FN 30854	GU646978	Campeche, 10 km N El Refugio	Mexico
6	*H. desmarestianus*	ROM 96089 = FN 29880	GU646979	Campeche: 25 km N Xpujil	Mexico
2	*H. desmarestianus*	ASNHC 3515 = LAF 1689	GU646980	Chiapas, 12 km N (by road) Berriozábal	Mexico
2	*H. desmarestianus*	ASNHC 1424 = ASK 660	GU646981	Chiapas, 12 km N (by road) Berriozábal	Mexico
2	*H. desmarestianus*	ASNHC 1425 = ASK 689	GU646982	Chiapas, 12 km N (by road) Berriozábal	Mexico
4a	*H. desmarestianus*	ASNHC 1426 = ASK 51	GU646983	Chiapas, 6.6 km S Palenque	Mexico
4b	*H. desmarestianus*	ASNHC 5826 = ASK 49	GU646984	Chiapas, 9.0 km S Palenque	Mexico
4c	*H. desmarestianus*	ROM 96096 = FN 29887	GU646985	Chiapas, 12.5 km S Palenque	Mexico
4c	*H. desmarestianus*	ROM 96105 = FN 29896	GU646986	Chiapas, 12.5 km S Palenque	Mexico
4d	*H. desmarestianus*	ASNHC 1440 = ASK 29	GU646987	Chiapas, 1.2 km E Ruinas de Palenque	Mexico
4d	*H. desmarestianus*	ASNHC 1441 = ASK 31	GU646988	Chiapas, 1.2 km E Ruinas de Palenque	Mexico
3a	*H. desmarestianus*	ROM 97542 = FN 33018	GU646989	Chiapas, 6 km E of Rayon, 1,560 m	Mexico
3b	*H. desmarestianus*	ASNHC 1431 =	GU646990	Chiapas, 9 km SE Rayon	Mexico

		ASK 589			
3b	*H. desmarestianus*	ASNHC 1432 = ASK 591	GU646991	Chiapas, 9 km SE Rayon	Mexico
7	*H. desmarestianus*	ROM 97520 = FN 30995	GU646992	Quintana Roo, 1 km N Noh-Bec	Mexico
7	*H. desmarestianus*	ROM 97521 = FN 30996	GU646993	Quintana Roo, 1 km N Noh-Bec	Mexico
1b	*H. desmarestianus*	CM 79530 = DSR 934 = AK 3108	GU646994	Oaxaca, Vista Hermosa, 1,000 m	Mexico
1b	*H. desmarestianus*	MVZ 161230 = DSR 1686	GU646995	Oaxaca; Distrito Ixtlán, Vista Hermosa, 1,000 m	Mexico
16	*H. desmarestianus*	ROM 112284 = F 48170	GU646996	Esteli, Esteli	Nicaragua
39	*H. nelsoni*	BYU 20644 = DSR 7189	GU647014	Chiapas, Cerro Mozotal, 15º25.866'N, 92º20.274'W, 2,930 m	Panama

CONCLUSIONS

The present studies of the mammalian fauna of the Caribbean lowlands of Costa Rica show a complex assemblage of animals with unique biology and diverse ecological histories. Each chapter deals with specific questions that allow us to address the broader questions posed by this dissertation. Secondary forests can be of great conservation value for non-volant mammals; no evidence of habitat preferences or community composition between primary and secondary forest were noted, at least not within the context of secondary forest types within La Selva (Chapter 1 and Chapter 2).

Herein, I document that the non-volant mammals have been, and continue to be, affected by anthropogenic disturbances at various spatial and temporal scales. Although secondary forests can hold complex assemblages of non-volant mammals, they can differ in a variety of biotic and abiotic factors, seemingly influencing behavioral responses among these forest types for some species (Chapter 1 and Chapter 2). Additionally, changes in densities of collared peccaries at La Selva are likely due to a combination of factors, including the extirpation of white-lipped peccaries (*Tayassu pecari*) from the area (Chapter 2). The spatial patterns observed for collared peccaries is telling of the conservation challenges faced in the Neotropics. Collared peccary populations have been affected by anthropogenic disturbances throughout this landscape in different manners. In many areas, hunting, among other factors, has contributed to low densities of peccaries, whereas in La Selva, where this species is abundant, human presence is affecting the habitat use of the species (Chapter 2).

Patterns of habitat use for rodents varied greatly throughout the region. Species occupancy and nightly trap success differed among forest fragments with various degrees of size, isolation, and edge-to-forest ratios (Chapter 3). Relative abundances for all species, and for spiny pocket mice (*Heteromys desmarestianus*), were higher in fragments of larger area (> 9 km^2) (Chapter 3). Population characteristics for the spiny pocket mice, such as mass and sex ratio, did not differ among large and small fragments (Chapter 3). Specifically, these analyses document that fragmentation, and other biotic and abiotic factors, may have large effects on the low-density populations of rodents in the area. As we aim to increase connectivity among forest fragments, it is essential to understand population structures so we can effectively monitor them.

Strip censuses conducted at La Selva Biological Station demonstrate that this methodology is extremely useful in studying Neotropical communities, although it targets some species better than others (Chapter 1). Sampling should be conducted both diurnally and nocturnally to gain a holistic understanding of assemblages because little overlap exists between species seen during the daytime and nighttime (Chapter 1 and Chapter 2). While such surveys are easy monitoring tools, considerable effort is required to achieve stable estimates and short term (i.e., several days) estimates are likely to produce unrepeatable results (Chapter 2). Increasing the number of observers on a trail does not affect the rate of detections, consequently, increased sampling effort with more observers should focus on walking different trails concurrently (Chapter 1 and Chapter 2). Data from these surveys provide valuable information to study the biology of particular species as well as to track changes in abundances over time.

Aspects of the biology and reproduction of species of interest are necessary to understand and implement conservation programs. I found sex ratios of adult *Heteromys desmarestianus* and *Nyctomys sumichrasti* to be 1:1 (Chapter 3 and Chapter 4). Reproduction for *N. sumichrasti* occurs year round, and they can rapidly produce successive litters. Litter size is small, and embryos are not necessarily evenly distributed across the uterine horns. Most females are parous by 60 g, although this can be quite variable (Chapter 4).

Finally, the biodiversity of the Caribbean lowlands is not yet fully understood. As has been shown herein, this area likely holds a currently unrecognized rodent species (Chapter 5), which may actually be part of a broader biogeographic pattern for rodents that has not been noted previously. Rodent species in the Caribbean lowlands are largely understudied, and populations from this area have been typically excluded from phylogenetic analyses. As we learn more about the unique patterns found in the Caribbean lowlands for various species, rodents may actually provide valuable data to better understand the evolutionary history of Central America.

The non-volant mammal communities in the Caribbean lowlands of Costa Rica are fairly representative of the assemblages that were present at the time of European settlement. In the last half of the 20th century, rapid habitat changes diminished the available land to maintain suitable populations of many important species. Additionally, other anthropogenic stressors, such as climate change and the application of aerial pesticides and fungicides by continuously growing banana and pineapple plantations, may begin to exert strong influences on these populations and test their long-term viability. Large and small scale projects, aiming to increase the amount of forest cover and connectivity in the landscape will be beneficial to these communities. Additional studies are essential to: 1) further elucidate the patterns of population fluctuations at longer time scales, 2) study the effects of fragmentation on the behavior and ecology of these species, and 3) determine parameters needed for the successful construction and maintenance of biological corridors. In sum, the approaches developed in these studies have proven valuable in characterizing the ecological differences and similarities of various species, providing robust data on these populations, informing us of the advantages and disadvantages of using particular methods, and presenting a framework focused on various spatial and temporal scales to appreciate the ecological history of these forests.