A comparison of seedling diversity and abundance in the range of howler monkeys (Alouatta palliata) in Bocas del Toro, Panama

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A COMPARISON OF SEEDLING DIVERSITY AND ABUNDANCE IN THE RANGE OF HOWLER MONKEYS (*ALOUATTA PALLIATA*) IN BOCAS DEL TORO, PANAMA

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Presented to

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of the Requirements for the Degree

Master of Science

Primate Behavior and Ecology

by

Erin Connelly

May 2017
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ABSTRACT

A COMPARISON OF SEEDLING DIVERSITY AND ABUNDANCE IN THE RANGE OF HOWLER MONKEYS (*ALOUATTA PALLIATA*) IN BOCAS DEL TORO, PANAMA

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May 2017

In this study, I investigated the potential effect of howler monkey (*Alouatta palliata*) defecations on the diversity and abundance of seedlings on the forest floor of a tropical lowland forest in Bocas del Toro, Panama. I conducted follows on a howler monkey group for 18 days and found six trees the monkeys used for sleeping. During this time, I collected feces and extracted the ingested seeds. I counted the seeds and identified the seed genus when possible. After this initial observation period, I constructed transects in random directions covering the entire tree crown underneath sleeping trees. I collected and counted every dicot seedling shorter than 30 cm. I identified the seedlings in the lab, to the species level when possible, and repeated the process in control transects of the same size in the same forest type, with comparable canopy cover and soil conditions. In total I identified 46 morphotypes from 967 individual seedlings, 676 underneath sleeping trees and 291 in control areas. Of the 46 morphotypes, I identified 16 to the species level, ten to the genus level, four to the family level, and 16 remain unidentified. Of these species, 12 were found exclusively in the
sleeping transects, and 11 were exclusive to the control transects. I predicted that there would be greater individual seedlings and greater species richness, and diversity underneath the sleeping trees than in control areas. I also predicted that some plant species would be more prevalent underneath sleeping trees due to howler monkey dietary preferences and what was fruiting during this period. I did not observe a significant difference in seedling abundance, species richness, Shannon-Wiener diversity, or Gini-Simpson diversity (p values > .05). Taking into account the life history of some clumped seedling species, I attempted to determine whether they arrived there via howler monkey endozoochory. I also examined the effects of secondary dispersers such as dung beetles and rodents, and offer suggestions for strengthening this research for future study. This study contributes to our knowledge of how howler monkeys contribute to forest flora communities, and offers an important foundation for the forest floor community for other students interested in primate seed dispersal.
ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION

Neotropical primates interact with fruit in a variety of ways, and among the most important of these is frugivory. There is evidence that primates move an enormous quantity of seeds through ingestion (Russo & Chapman, 2011), and howler monkeys are no exception. In one study, a howler group (*Alouatta seniculus*) in Colombia moved 290,174 seeds from 48 species in only 60 defecations (Giraldo, Gómez-Posada, Martinez, & Kattan, 2007). Another study in Mexico found a howler group (*Alouatta pigra*) to move 51,369 seeds from 16 plant species in 408 defecations (Zárate, Andresen, Estrada, & Serio-Silva, 2014). Yet another found a howler group (*Alouatta seniculus*) in French Guiana dispersed more than 1,000,000 seeds in just one year of observation (Julliot, 1997). It is little disputed that howler monkeys can and do disperse seeds, but the quality of this dispersal, and how successful it is for the seeds, remain important questions in ecology.

Howlers deposit seeds in specific clumping patterns underneath trees they sleep in for many years (Bravo, 2011; Julliot, 1992, 1997), and historically ecologists have assumed that the seed mortality related to a high volume of dung is high. There is some evidence that dung attracts rodent seed predators (Andresen, 2002), so this may play a role. However, there is little evidence that seed density is a problem for seed mortality, and instead, research indicates that these areas of clumped defecation (latrines) are nutrient rich, and may be a near
ideal locations for seedling germination (Feeley, 2005). Thus, howlers create nutrient-rich areas of repeated defecation in specific areas in the forest, known as latrines.

In 2009, Pouvelle investigated this “latrine effect” on the seed bank underneath howler sleeping trees, and found that indeed, the soil in these areas had greater abundance, species richness, and diversity of seeds than in control areas. Julliot (1992) and Bravo (2011) found corroborating results in seedling abundance, richness, and diversity in French Guiana with *A. seniculus* and in Southern Argentina with *A. caraya*.

*A. palliata* is the most widespread of the howler species (Crockett, 1998), inhabiting the widest variety of habitats and forest types. Most of the research on howler monkey seed dispersal occurs in the wet forests of South America (Russo & Chapman, 2011), and most of the diet studies for howler monkeys occur in the dry seasonal forests of Mexico and Costa Rica (Dias & Rangel-Negrín, 2013). I aim to fill a geographic gap in the literature by recreating parts of Bravo, Julliot, and Pouvelle’s studies with a new howler species, *A. palliata*, in the Bocas del Toro region of Panama. The island chain has a robust howler monkey population that is understudied compared to populations in Mexico and Costa Rica. Long-term studies on howler monkeys have occurred on Barro Colorado Island (BCI) in Lake Gatun, but scientists have not produced a howler monkey seed dispersal study. Mine is the first study of its kind for this species in this region.
I hypothesized that the latrines underneath howler sleeping trees are areas of successful germination and seedlings exist in greater abundance, richness, and diversity in these areas compared to other areas in the howler monkey’s range. These results would be consistent with those of other howler seed dispersal studies on different howler species in South America.
CHAPTER II
LITERATURE REVIEW

Introduction to Seed Dispersal

Neotropical plant species have a variety of strategies for seed dispersal, and significant among these is endozoochory: seed dispersal via ingestion by frugivorous animals. In tropical forests, animals interact with 90-95% of seeds (Jordano, 2000; Terborgh et al., 2002), and some 75% of trees produce fruits, presumably for endozoochorous seed dispersal (Fleming & Kress, 2011; Howe & Smallwood, 1982). Typically, scientists consider birds the most essential seed disperser of the tropics, but primates also consume fruits and ingest their seeds. Understanding the impact of mammals on plant ecology is vital if we are to better understand their complex ecological relationships with their forest homes (Jordano, Garcia, Godoy, & Garcia-Castazño, 2007). Seed dispersal is of utmost importance to the endozoochorous plant that expends energy growing fruit to attract a suitable dispersal agent, and the frugivorous animal benefits as well by consuming the fruit. But the extent to which this interaction is wholly mutualistic is not well understood, and determining the seed dispersal effectiveness of plant strategies and dispersal agents, such as primates, is an important aspect of studying tropical forest ecosystems (Schupp, Jordano, & Maria-Gomez, 2010).

Howe and Smallwood (1982) outlined dispersal mechanisms and the advantages for seed dispersal. Since their paper was published, the field of seed dispersal research has grown immensely, and much of the subsequent research has
been conducted using the framework of their hypotheses. Today, the article remains valuable for understanding many key concepts of seed dispersal. Seeds are mainly dispersed by animals (zoochory, not to be confused with dispersal by animal ingestion, endozoochory), by the wind, by water, or by simply exploding (self-dispersal). Further variation exists within these broad categories; for example, plants tempt animals to their seeds both by growing nutritious fruits and by emitting chemical attractants, as well as mechanisms that do not involve ingestion, such as sticky barbs that cling to the coats of passersby. The process of a seed dispersing from its parent, germinating, growing, and ultimately surviving to reproductive adulthood is known as recruitment. Accurately predicting seed recruitment is key to understanding plant population ecology and the role of seed dispersal.

There are three advantages for a plant to disperse its seeds, none of which are mutually exclusive. One advantage, described by Janzen (1970) and Connell (1971), is the “escape hypothesis.” This hypothesis proposes that seeds will disperse if mortality is higher near the parent plant. Higher rates of mortality are attributed to a variety of potential factors: perhaps parent plants attract increased seed/seedling predators, pathogens, or fungi, or there is density-related competition among seedlings (Howe & Smallwood, 1982). Today, evidence varies, and it is hard to generalize the strength of the Janzen-Connell effect, as it is now known. Instead, the Janzen-Connell effect acts on seedling mortality in context-specific ways. Research suggests that the effect is strong in some plant
families and environments or during some life stages of the plant (Petermann, Fergus, Turnbull, & Schmid, 2008; Martin & Canham, 2010; Liu, Liang, Etienne, Wang, Staehelin, & Yu, 2011; Sheffer, Canham, Kigel, & Perevolotsky, 2013).

However, other research shows mixed or neutral support for the hypothesis in different circumstances (Luo, Mi, Chen, Ye, & Ding, 2012; Takeuchi & Nakashizuka, 2007; Theimer, Gehring, Green, & Connell, 2011). Confirmation of the “escape hypothesis” and the Janzen-Connell effect must quantify the rates of recruitment as the seeds travel farther from the parent trees, and determining plant paternity remains a challenge.

Another advantage described by Howe and Smallwood (1982) is the ‘colonization hypothesis’, which predicts that the most favorable sites for seedlings are unpredictable in time and space, and therefore widespread seed dispersal is critical for plant survival. Habitat quality changes over time, and this theory is supported by plants that can quickly colonize habitats that have been recently disturbed by natural disasters such as storms or landslides. In this case, distance from the parent tree is not relevant to the survival of the seed in terms of density dependent mortality, as conditions around the parent plant may change over time, or the parent plant may contribute to survival and success in unpredictable ways.

The third hypothesis discussed by Howe and Smallwood (1982), and the theory most relevant to primate seed dispersal, is the “directed dispersal hypothesis,” in which “dispersal agents take seeds to nonrandom places that are
well suited for establishment and growth” (p. 209). In order to support this hypothesis in primates, the habitats, sites, and even microsites where the animals deposit seeds would need to demonstrate higher rates of seedling survival. Evidence that primate feces are nutrient rich (Feely, 2005) and that the areas in the forest where primates habitually defecate, hereafter, primate latrines, are areas of successful germination (Pouvelle, Jouard, Feer, Tully, & Ponge, 2009) would support this hypothesis. Evidence that clumps of feces deposited by primates attract seed predators (Russo, 2005) would disprove this hypothesis.

Howe and Smallwood (1982) note that the above advantages to seed dispersal are not mutually exclusive, and it is likely that all these hypotheses (and even others) act on a seed depending on the specific context and dispersal agent species. Seed dispersal studies take each into account to quantify the effectiveness of the disperser (Chaves, Stoner, Arroyo-Rodríguez, & Estrada, 2011; Pouvelle et al., 2009; Martins, 2006; Jordano et al. 2007). Most often, researchers measure seed dispersal effectiveness as defined by Schupp in his 1993 review, updated in 2010. The original framework for seed dispersal effectiveness (SDE) focused on the extent to which a dispersal agent, usually an animal, contributes to the success of a plant species (Schupp, 1993). From the perspective of the plant, effectiveness has two simple variables: quantity of dispersal and quality of dispersal (Schupp et al. 2010). The way in which seeds are successfully dispersed impacts recruitment, density, plant diversity, and all aspects of plant population dynamics (Schupp et al. 2010; Jordano et al. 2007), which ultimately affects the spatial distribution of
animal populations as well, making SDE just one method to study the complex ways frugivores and folivores interact with their preferred plant species (Jordano et al. 2007).

Understanding the role animals play in the ecology of the Neotropical rainforest has important consequences for forest conservation and regeneration, and historically, most of this research has focused on birds. Using fossil evidence, Fleming and Kress (2011) hypothesize that angiosperms began to develop small fruits during the Cretaceous period (145.5-65.5 mya), and that biotic dispersal, including frugivory in birds, coevolved with fruits later in the Eocene (55.8-33.9 mya). This relationship then helped facilitate frugivory in primates. Thus, frugivory is much more common, and potentially older, in birds than other animals, but today, bats and some other mammals, including primates, are also considered essential dispersers in the Neotropics (Fleming & Kress, 2011). Until recently, researchers have presumed that primates are not as important or effective as seed dispersers when compared to birds and bats. One reason for this bias may be that in some species, for some plants and in some contexts, primates are known seed predators (e.g., Lagothrix, Stevenson, Pineda, & Samper, 2005; Ateles and Alouatta, Stevenson, Castellanos, Pizarro, & Garavito, 2002; Pitheca and Chiropotes, Kinzey & Norconk, 1993; Colobus, Poulsen, Clark, & Smith, 2001; Eulemur; Overdorff & Straight, 1998). Another reason ecologists have presumed primates are not ideal dispersers is their tendency to disperse large clumps of feces, which may attract seed predators and lead to lower seed survival rates.
(Russo, 2005; Howe & Smallwood, 1982). In the last few decades, more researchers have questioned these assumptions, and we now recognize that primates process fruits in a variety of ways, among these, seed spitting, seed dropping, seed predation, and seed swallowing (Lambert & Garber, 1998). We now recognize that some species of primates across the order can be, and are, important seed dispersers in context-specific ways (Russo & Chapman, 2011; Lambert, 2010; Anzures-Dada, Andresen, Martínez, & Manson, 2011; Martins, 2006; Kone, Lambert, Refisch, & Bakayoko, 2008; Benítez-Malvido, 2014; Chaves et al., 2011). This range of interactions between plants and primates, combined with the sheer variety of plant species a primate may interact with (Alouatta alone is known to handle 1,165 plant species in 479 genera, Dias & Rangel-Negrín, 2013), make it difficult to generalize the seed dispersal effectiveness of any given genus. In their chapter from the textbook Primates in Perspective, Russo and Chapman provide a comprehensive review of this variation, and the ways in which primates affect the “forest community structure” (Russo & Chapman, 2011, pp. 510) via seed dispersal and its consequences for forest conservation in the absence of primates.

Introduction to Howler Monkeys (Alouatta spp.)

According to Cortés-Ortiz, Rylands, & Mittermeier (2015), nine species comprise the genus Alouatta, with another three tentatively acknowledged (pending additional genetic and/or morphological information). The folivorous,
opportunistically frugivorous howler monkey is native to 19 countries throughout the Neotropics, from southern Mexico to southern Brazil, and occupies the largest range of any neotropical primate (Crockett, 1997). In the absence of hunting pressure, howlers can be successful in forest fragments and in close proximity to humans and agriculture (Arroyo-Rodriguez & Dias, 2010). This is largely due to their ability to thrive at many altitudes (between sea level and ≥ 2500 m) in diverse forest types, and their small home ranges (<25 ha), reliance on folivory, and low metabolic requirements (Crockett, 1997). Howlers can persist in areas where other large-bodied monkeys, such as spider monkeys (Ateles spp.) and woolly monkeys (Lagothrix spp.) cannot (Estrada, Raboy, & Oliveira, 2012), making understanding the ecological role of howlers, especially in degraded habitats, a high priority for conservationists, ecologists, and primatologists alike.

Howlers have a vast dietary repertoire, consuming 1,165 known plant species in 111 families (Dias & Rangel-Negrín, 2013). Although howlers are leaf specialists and are considered the most folivorous of all New World monkeys, they exhibit great dietary flexibility, and as a genus are known to consume up to 548 fruit species (Dias & Rangel-Negrín, 2013), making up 50% of their diet when available (Silver, Ostro, Yeager, & Horwich, 1998). Howlers typically consume fruits seasonally, and the most common of these fruits are from only a few plant families: figs (Moraceae), legumes (Fabaceae), laurels (Lauraceae), and zapote (Sapotaceae), from trees they visit over many years (Dias & Rangel-Negrín, 2013; Arroyo-Rodríguez, Andresen, Bravo, & Stevenson, 2014; Bicca-
Additional evidence for howler seed dispersal includes their tendency to swallow and later defecate most of the seeds they handle (Arroyo-Rodríguez, et al., 2014) (although they do occasionally act as seed predators (Stevenson et al., 2002)), and may have a preference for fruits with large seeds, of which they can be the sole disperser if those seeds are too large for birds or sympatric primates to swallow (Benítez-Malvido, Gonzáles-Di Perro, Lombera, Guillén, & Estrada, 2014; Cramer, Mesquita, & Williamson, 2007). These qualities, as well as their status as the most common primates in both intact and degraded New World forests (Crockett, 1997; Bicca-Marques, 2003), give howlers the potential to be important seed dispersers for some plant species. Seed dispersal effectiveness is measured by the quantity and quality of seed dispersal (Schupp et al., 2010), and although the SDE of howler monkeys is not well understood, several studies have examined the quantity of seed dispersal and likelihood of germination in howler-dispersed seeds, which I will review here.

Two factors in determining the likelihood of germination is the effect of gut passage and the digestive cycle of the dispersal agent, in this case, howler monkeys. Seeds that pass through the howler gut remain viable (Milton, 1980; Estrada & Coates-Estrada, 1984; Julliot, 1997; Andresen, 2002; Bravo, 2011) despite howler digestion being very slow compared to other primates. Benítez-Malvido et al. (2014) compared gut passage time and germination rates between spider monkeys and howlers and found that spider monkeys (Ateles spp.) passed seeds in 2-6 hours, whereas the sympatric howlers required 18-33 hours. The
authors partially attribute this slow digestion to an elongated gut that helps howler monkeys break down cellulose, a difficult to digest, high fiber material found in the leaves that make up more than 50% of the howler monkey diet. Either despite or possibly because of the long gut passage time, the authors found that the seeds ingested by the howlers were more likely to germinate than the spider monkey dispersed seeds.

Traveset, Rodríguez-Pérez, & Pías, (2008) report that animal gut passage affects seeds in two ways: through scarification and deinhibition. Scarification is the process by which the seed coat is removed or weakened, and deinhibition is the separation of seeds from the fruit pulp. Ingestion of seeds is not necessary for deinhibition, as seeds may be separated from their pulp after being spat or handled, and the likelihood of germination in seeds handled but not ingested by howler monkeys is not known (Arroyo-Rodríguez, 2014). Scarification typically occurs as a result of digestion and can aid germination by rendering seeds more permeable to water, gasses, and nutrients (Traveset et al., 2008). Germination trials have been performed with several howler species, and the results are mixed. Some studies show a positive effect of howler gut passage on germination rates (Julliot, 1997; Estrada & Coates-Estrada, 1984; Andresen, 2002; Bravo, 2011), other studies show a neutral effect (Martins, 2006; Julliot, 1996) and still others show a negative effect (de Figueriredo, 1993; Graeff, Bicca-Marques, & Astarita, 2007). However, a fairly definitive analysis of neotropical germination published by Fuzessy, et al. in 2016 synthesized data from 19 published germination studies.
They found that germination increased by 34% when passed by folivore/frugivores, like howlers, and germination time reduced by 27%. While these rates were not as dramatic as the strict frugivores, (75% higher germination rates, but no effect on germination time), their results offer compelling evidence that passage through the gut of howler monkeys has a positive effect on germination. One particularly interesting result of Fuzessy, et al.’s analysis is that seeds ingested by folivore/frugivores germinated faster than those of pure frugivores. This could be a result of a fertilization effect of feces or perhaps a response to potentially increased seed predation when deposited with the feces of folivores. The question of why seeds germinate faster after passage through howler guts, offers an important new avenue of inquiry.

The presence of arthropod larvae infesting seeds is another factor in the howler digestive process, and is a greater factor for some plants (particularly the *Ficus* family, which is pollinated by wasps) than others. Bravo (2008) investigated the effect of howler digestion on the insect infested seeds of *Ocotea diospyrifolia* (family Lauraceae). She found a fairly complex relationship between seeds, insects and the monkeys, but that howler digestion successfully killed insect larvae when the fruit was consumed early in the larval life stage, and those seeds successfully germinated. Later in the larval life stage when the fruits were riper, howler digestion did not kill the larvae, and the seeds did not successfully germinate, although the larvae were spread. In two other plant species, *Eugenia punicifolia* (family Myrtaceae) and *Banara arguta* (family Salicaceae), infested
seeds were destroyed with the larvae during digestion, but uninfested seeds were likely to germinate. Bravo concluded that howler preferred fruit species that are also infested by insects at various times of the year can have several outcomes depending on the fruit species and when the fruit is consumed. This is certainly an area that warrants more study, especially because *Ficus* is an important howler food source and is pollinated by wasps that may affect dispersal (Bravo, 2008). From a dietary perspective, if howlers are consuming insects intentionally or unintentionally, this potential protein source should be explored further.

Much remains unknown about the quality of howler seed dispersal (Anzures-Dadda et al., 2011; Benítez-Malvido et al., 2014). Seed dispersal quality is affected by many factors pre- and post-dispersal. Pre-dispersal factors include how the seeds are handled: whether they are spit, swallowed, dropped, or killed on (Schupp et al. 2010). Other studies evaluate the effect of gut passage and dispersal distance (Benítez-Malvido, 2014). Post-dispersal factors include the effect of the dispersal pattern, the effect of clumping, the presence or absence of dung, and the effect of secondary dispersers, such as rodents and arthropods (Schupp et al. 2010; Howe & Smallwood, 1982). Evidence shows that howlers defecate in latrines, typically underneath sleeping trees (Bravo, 2011; Julliot, 1997), and in 2002, Andresen investigated the effect of this clumping pattern on dispersal effectiveness. In Brazil’s central Amazon, she found that over 25 months, the howler monkeys (*Alouatta caraya*) dispersed 137 plant species, mainly for families Sapotaceae, Moraceae, and Leguminosae. The Sapotaceae
seeds, in particular, are large (33 mm in length x 18 mm in width), and it is likely that howlers are their primary, possibly only, disperser, because such large seeds can only be swallowed by large-bodied arboreal species. Andresen’s results are particularly striking in the context of influential, earlier studies of howler frugivory that record howlers consuming approximately 40 plant species (Milton, 1980; Coates-Estrada & Estrada, 1984). Her research confirmed the clumped defecation pattern researchers had previously observed, and she recorded that 61% of defecations occurred near sleeping trees. Finally, Andresen found that rodents were more likely to kill on seeds in higher density dung piles, and predation was lowest on seeds in piles with little to no dung. Dung beetles were more likely to bury seeds deeper (possibly too deep for germination, but this threshold is not known) in defecations with greater amounts of dung. Andresen concludes that in this region of the Amazon, due to the large variety of seed species present in their feces, howlers are probably effective dispersers at the community level, and that differences in fruit consumption between studies are related to forest composition. Andresen indicates that group size varies in howler species (Crockett, 1997), and that smaller groups may be able to take advantage of more and different fruit species. Alouatta palliata, in particular, typically has the largest groups, and finding sufficient fruit resources for many individuals represents a unique foraging challenge for that species and may result in increased folivory (Dias & Rangel-Negrín, 2013).
Martins (2006) examined similar questions, this time in Southeastern Brazil and with brown howlers (*A. guariba*). She recorded how many seeds were found, from which species per defecation, and the size of those seeds. In this study, howler defecations contained a mean of 18 seeds per defecation but only 1-2 tree species per defecation (in 147 fecal samples), which was much lower than what Andresen found. Martins attributes this characteristic to the howlers’ preference for folivory. The seeds tended to be large (>2 mm), and she compared the quantity and germination rates with those of sympatric *Brachyteles*. Between the two species she found no difference in germination rates (despite drastic differences in gut passage time). She concluded that her results support those hypotheses that emphasize the importance of large-bodied monkeys for the dispersal of large seeds, and that howlers can contribute to the recruitment of these seeds in some specific tree species.

Another examination of seeds and seed species per defecation by Giraldo et al. (2007) found that high altitude red howlers (*A. seniculus*) in Colombia distributed a mean of 2.3 seed species per defecation and a total of 290,174 seeds in 60 defecations. In total, 99.9% of these seeds were less than 5 mm long. The authors observed the howlers consuming only 48 species of trees (nine were fruit trees) over the course of six months. Again the howlers contributed a relatively low number of tree species to forest composition, but in this case, the howlers were located in fairly degraded and partially fragmented secondary forest. Consistent with other howler diet studies, Moraceae was the most important fruit
tree family in the howlers’ diet, with genera *Ficus* and *Cecropia* being an especially high proportion of total Moraceae seeds. The authors conclude that the howlers are probably effective seed dispersers for at least nine fruit species present in feces, partially due to the sheer number of seeds they dispersed. The authors note that their population was found at high altitude in a secondary forest, which may account for the low number of fruit species compared to lowland populations.

In a degraded landscape, an agricultural zone, Zárate, Andresen, Estrada, and Serio-Silva (2014) compared dietary plant diversity and rates of seed dispersal between rainforest-dwelling troops of black howlers (*Alouatta pigra*) and troops living on a cocoa plantation in Southern Mexico. The authors found that the groups differed in seed dispersal quantity and the size of the seeds dispersed. The group on the cocoa plantation had less dietary diversity than the forest groups and dispersed 51,369 seeds from 16 plant species, which were mostly small (4% > 3 mm in length), whereas the rainforest group dispersed 6,536 seeds from 13 plant species, which were larger (78% > 3 mm in length). The authors explained this dramatic difference by resource availability in the two habitats. The cocoa farm group had access to fewer tree species with smaller seeded fruits. The rainforest group had access to a greater variety of tree species, and therefore consumed fewer fruit species, but their preferred fruits had larger seeds. Here the data suggest that howlers may not be effective as dispersers for large-seeded fruits compared to small-seeded fruits. However, the authors
conclude that the howlers can be effective dispersers for small-seeded fruit trees in agricultural spaces, and large-seeded fruits are preferred when available, thus making them somewhat effective dispersers for those species.

Counting seedlings is a method of measuring the likelihood that howler dispersed seeds will germinate, which is an important factor in determining seed dispersal quality. Julliot (1997) identified and mapped the seedlings of howler (Alouatta seniculus) dispersed tree species in the primary rainforest of French Guiana, to investigate germination and dispersal patterns. She plotted the seedlings (<1m tall) of six fruiting plant species, which represented 17% of her troop’s diet, in grids in ten plots within the home range of the troop. She found 1,209 seedlings under the sleeping trees and only 312 in the control plots. Of these seedlings, five of the six species surveyed had four times higher densities under sleeping sites than in the control sites. This study makes a clear and compelling argument that not only are howler monkeys effective seed dispersers for at least the surveyed plant species, but that they clump these seedlings in specific places, contributing to floristic heterogeneity of the rainforest.

In a similar study, Bravo (2011) analyzed the recruitment of saplings of howler preferred fruit tree species in Northern Argentina. She compared sapling recruitment in areas under sleeping trees within the ranges of five howler monkey (Alouatta caraya) groups. She designated these areas as large latrines, small latrines, and control plots (random areas). She found that there were four times more saplings in latrines than in other areas, suggesting that seedling density
offsets any mortality factors underneath howler sleeping trees and other latrines in their ranges. This study provides further evidence that howlers contribute to a clumped dispersal pattern. Bravo surveyed plant species in 12 genera and found that howlers were most effective in dispersing family Myrtaceae, and that some plant species were more successful in the large latrines under sleeping trees than in small latrines. These results contradict traditional thinking in the field, namely that howlers are not effective seed dispersers due to their clumping patterns, lack of fruit specialty, and defecating seeds with large amounts of dung. Bravo and Julliot’s results both question the validity of those assumptions, and show that howler-dispersed seeds can successfully germinate and grow into saplings even in high densities and in conditions previously assumed to contribute to seedling mortality. How many of these saplings grow into fruiting, adult trees remains unknown. Additional questions from Bravo’s study include the extent to which howler seed dispersal is effective outside of large and small latrines. Howlers often deposit seeds outside of latrines: Bravo recorded that as much as 35% of defecations occurred outside latrines, meaning that howlers may be effective dispersers for plant species that recruit in low densities as well as plants that recruit in latrines.

This “latrine effect,” as dubbed by Pouvelle et al. in 2009, clearly shows that increasingly diverse seeds are dispersed underneath the sleeping trees of howler groups than in control areas, even after dung beetles have buried feces. Pouvelle and colleagues sampled the soil seed bank underneath sleeping trees and
in control areas. They found that seed richness, density, and diversity were all higher in defecation areas underneath sleeping trees after dung beetles had buried the feces. They conclude that howlers’ specific defecation patterns impact the distribution of small seeded species, and that more research on the germination and growth of these seeds is necessary to understand the true impact of the latrine effect.

Several studies have shown that howler monkeys disperse seeds in clumping patterns underneath sleeping tree sites (Julliot, 1997; Pouvelle, et al. 2009; Anzures-Dadda et al. 2011). In my study I provide data that contributes to this understanding of the quality of seed dispersal by measuring the abundance, species richness, and diversity of seedlings underneath howler sleeping trees.
CHAPTER III

METHODS

Study Site

I collected data at the Institute for Tropical Ecology and Conservation (ITEC) located on the Western tip of Isla Colón in the Bocas del Toro region of Panama (9°20’ N, 82°15’ W). The area receives a mean annual rainfall of 3,431.8 mm of rain per year and has a mean temperature of 25.5 °C. The island has two relatively dry seasons, mid-December through mid-May and August through October, and two rainy seasons, mid-May through July and November through December (Paton, 2015). The region has experienced an influx of development in the last 10 years, primarily driven by the growing tourist industry. This, combined with the island’s many residents who depend on subsistence farming, has led to a patchwork of dense forests, small farms, and hotels and resorts on Isla Colón. The most prevalent forest type on the island is classified as tropical lowland rainforest and is primary or secondary forest with canopies as high as 120 m. The forest at ITEC is a 60-ha forest fragment with limited canopy connectivity to neighboring forests and is surrounded mainly by subsistence farms, teak plantations, and cattle-grazing lands. There are some beaches on the island but mangrove forest dominates the islands’ perimeters, including Isla Colón. I recorded rainfall from 7/8/16 – 8/9/16 in cm daily using the station’s rain gauge.

Initial Observation Period
Upon arrival at the site, I enrolled in a 4-week Tropical Rainforest and Canopy Ecology course, which oriented me to the trail systems and ecosystems on the island. I used this time to familiarize myself with the GPS equipment, learn the trail systems, and practice identifying plant species using a dichotomous key. By recording early morning howling bouts, I determined that the site had four howler groups (*Alouatta palliata*), and I performed 7 consecutive day-long follows on one of the groups to determine its home range and familiarize myself with its members. The group was well habituated and comprised of 12 monkeys: three adult males, eight adult females, and one juvenile of undetermined sex. Approximately halfway through data collection, an infant of undetermined sex was born to the group. Howler monkeys are monochromatic, but males are easily identified by their loud calls, expanding throat sacs, and pendulous white testes. They are also slightly larger than their female counterparts (Milton, 1980). See photos of some group members in Appendix A.

To determine the fruit tree species that were likely to have been dispersed by the monkeys, I identified seeds in the howlers’ defecations. I began data collection by locating the group pre-dawn (~0600 h). Upon arrival at the sleeping tree, I marked its position in GPS, used flagging tape to mark the tree, and measured and recorded its diameter at breast height (DBH). I considered it a sleeping tree if I saw minimum three individuals in the tree. I also attempted to identify the tree species using the Princeton field guide *Trees of Panama and Costa Rica* (2011). Often, tree ID in the field could not be confirmed, so I took
photos of the leaves, bark, and fruit (if present), and collected a mature leaf and
branch samples in plastic bags labeled with the date and time for later
identification at the on-site laboratory. The lab housed extensive guides to the
local flora, and in addition to the above Princeton guide, I relied heavily on Alan
Gentry’s *A Field Guide to the Families and Genera of Woody Plants of Northwest
South America (Colombia, Ecuador, Peru) with Supplementary Notes on
Herbaceous Taxa* (1996) and *The Kew Tropical Plant Families Identification
Handbook* by Utteridge and Bramley (2014). In the lab I also accessed the
Smithsonian Tropical Research Institute’s Herbarium online, which has
documented the plant species of Panama since the 1930s. Some days the group
slept in a sleeping tree I had previously identified, and some days I could not find
the group.

I collected as much feces as possible from the morning defecations in
plastic bags labeled with the date. When possible, I identified the age and sex
class of the monkey which defecated. I then followed the group for several hours
to their first feeding tree to confirm the group’s identification based on their home
range and the presence of two distinct individuals (one adult male with scarred
testicles, and one adult female with two large bot fly scars on her face). I
considered group identification confirmed if I could identify one of these
individuals and if they were within their known range. After group confirmation, I
returned to the lab to analyze the feces on the same day of collection. I used the
following procedure: 1) weighed the sample, 2) washed the defecation through a
sieve to separate all seeds, 3) counted all seeds per defecation event, 4) identified the seeds to the genus level (species level if possible) by comparison to on-site local seed and plant reference guides listed above and the Smithsonian Tropical Research Institute Herbarium catalog, and 5) photographed and recorded all seeds, their sizes, and the dates I collected them (See Appendix B). I separated the seeds into size categories based on the longest point. Seeds < 3 mm were small, 3 – 10 mm were medium, > 1 cm were large, and one Spondias seed measured > 2 cm, which I categorized as extra-large. As I identified the seeds in the defecations, I entered them into a table of observed defecated seed species. At the end of this initial observation period, I combined that table with a list of howler preferred fruits and common genera in the region.

I repeated these group follows and collected feces until I identified six sleeping trees, which took 18 days.

Transects

Following this initial observation period, I constructed transects underneath the sleeping trees and in control areas. To make the transects, I stood underneath the middle of the tree crown (in most cases at or near the trunk) and measured as long as the entire tree crown (shortest: 14 m, longest: 18 m) in a direction randomly selected by dropping a pencil and making the transect in the direction it pointed. I located control transects parallel to the sleeping tree transects and in a random direction between 10 - 20 m from the edge of the tree.
crown, outside of the defecation area but in similar forest type in terms of vegetation and soil conditions. I used surveyor’s flags to mark the boundaries of each transect. I repeated this process for each of the six sleeping trees and their corresponding control transects. I then evaluated and recorded the abundance, diversity, and density of all seedlings (< 1 m tall) in each transect that were not a palm or grass (i.e., dicots), because the woody, fruiting trees that howlers eat are exclusively dicots. In plastic bags labeled with the date and transect, I collected all seedlings, including as much of the roots as possible. I grouped individuals that I thought were the same species together into numbered morphotypes and labeled bags by number. In the lab I attempted to identify each seedling to the genus level, species level when possible. For this task I relied heavily on Nancy Garwood and Margaret Tebb’s comprehensive work: Seedlings of Barro Colorado Island and the Neotropics (Garwood & Tebb, 2009), which has a dichotomous key and detailed illustrations of approximately 3,000 neotropical species. See seedling samples and reference materials in Appendixes C and D. I entered the day’s data in a field notebook and transcribed those notes to an electronic copy on a personal computer each evening with backup to the cloud and a flash drive.

Data Analysis

I analyzed seedling abundance (seedlings/m²) and seedling diversity and compared these metrics between the sleeping tree plots and control plots. I used the statistical computing program R, package iNEXT (Chao, Hsieh, & Ma, 2014)
to calculate species richness, and Shannon-Wiener and Gini-Simpson diversity indices for each plot. Species richness ($p$) is the number of species present, an important number, but one that does not indicate how evenly distributed species are or any other way the species are organized. The Shannon-Wiener index is $H = -\sum p \ln p$. This index takes evenness into account by calculating the inverse of the sum of proportion times the natural log of the proportion ($p = \frac{n}{N}$, where $n$ is individuals in a species and $N$ is the total samples) (Magurran, 2004). As evenness and richness increase, $H$ increases (Magurran, 2004). The Gini-Simpson index is also known as a dominance index, because it weighs dominant species more heavily. Gini-Simpson diversity predicts the probability that two random samples from the same patch are the same species; as diversity increases, this index decreases. R package iNEXT reports the reciprocal Gini-Simpson index, so we can interpret $D$ as increasing with species richness where more dominant species are weighted more heavily (Chao et al. 2014). Gini-Simpson diversity ($D$) = $1 / \sum \frac{n (n - 1)}{N (N - 1)}$, where $n$ is individuals in a species and $N$ is the total samples of all species (Magurran, 2004).

I calculated the mean richness, Shannon-Wiener diversity, and Gini-Simpson diversity for the sleeping and control plots and used R package nortest to test for normality. Neither abundance data nor diversity data were normally distributed, so I performed a non-parametric paired Wilcoxon Signed-Rank test to determine whether there was a significant difference between the plot types. I used R package iNEXT to graph species accumulation curves for species richness,
and both diversity indexes separately in sleeping transects and control transects. I conducted paired Wilcoxon Signed-Rank tests to determine whether there was a significant difference between the species richness, Shannon-Wiener diversity, and Gini-Simpson index between the sleeping tree transects and control transects.

For the fecal samples, I calculated the mean weight in grams per defecation, the mean number and species of seeds per defecation, and the mean number of seeds per gram of feces.
CHAPTER IV

RESULTS

Seedlings

I identified 46 morphotypes from 967 individual seedlings. Of these morphotypes, I identified 16 to the species level, 11 to the genus level, 4 to the family level, and 15 remain unidentified. I found 12 exclusively in the sleeping transects, and 11 were exclusively in the control transects. For my sleeping transects $n = 676$ seedlings, and for my controls $n = 291$ seedlings. Seedling abundance was higher underneath sleeping trees than in control areas, with a mean abundance of 3.45 seedlings/m$^2$ in the sleeping areas, compared to 1.66 in control areas, (see Figure 1) but this difference was not significant ($p=.34$).

![Figure 1. Seedling abundance by sleeping tree.](image-url)
Dominant genera in both sleeping and control transects were *Inga*, *Ficus*, and *Siparuna*, and family Rubiaceae. See Table 1. I considered plants with seeds $\geq 1$ cm large seeded. I found nine large seeded species, and of these, *Chrysophyllum argenteum* was the only seedling present underneath sleeping trees but not found in control areas. *Spondias mombin*, whose very large seeds ($> 3$ cm) were present in feces, was absent in all of the transects. See Appendices C and D for photos of seedling samples and reference materials.
### Table 1. Found seedlings.

<table>
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<tr>
<th>Family</th>
<th>Genus/Species</th>
<th>Sleeping Trans.</th>
<th>Control Trans.</th>
<th>Condition</th>
<th>In bowler diet?</th>
<th>Type</th>
<th>Seed Size</th>
<th>Dispersal Mechanism</th>
<th>Reference(s)</th>
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<td>Silver et al. 1999; STRI Herbarium</td>
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Table 1. Found seedlings continued.

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<td></td>
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</tbody>
</table>

\( n = 967 \)
Species richness, Shannon-Wiener diversity, Gini-Simpson diversity values were all higher underneath sleeping trees than in control areas (see Figure 2), but this result was not significant (richness, $p = .21$; Shannon-Wiener diversity, $p = .56$; Gini-Simpson diversity, $p = .31$).

**Figure 2.** Mean diversity indexes between sleeping and control plots.

The species accumulation curves (see Figures 3 and 4) show that while richness would likely increase with more sampling, Shannon-Wiener diversity and Gini-Simpson diversity are accurate for both sleeping transects and control transects.
Figure 3. Species accumulation curves for sleeping transects where 0 = mean richness, 1 = mean Shannon-Wiener diversity, 2 = mean Gini-Simpson diversity

Total species richness: 37; Shannon-Wiener diversity: 11.99; Gini-Simpson diversity: 6.21

Figure 4. Species accumulation curves for control transects where 0 = mean richness, 1 = mean Shannon-Wiener diversity, 2 = mean Gini-Simpson diversity

Total species richness: 35; Shannon-Wiener diversity: 9.08; Gini-Simpson diversity: 5.95
Feces

I identified nine seed morphotypes from a total of 589 seeds. Of these morphotypes, I identified genus *Ficus* (family Moraceae), genus *Inga*, and species *Spondias mombin* (family Anacardiaceae). Overall, 52% of the seeds were *Ficus* (309/589) and 39% were an unidentified morphotype (218). The *Spondias* seed was characterized as extra-large in length (>2 cm) and was the only individual in that size category. Three seeds were large (1-2 cm), 269 were medium (3mm-1cm), and 309 were small (<2 mm). Of the small seeds, 100% were *Ficus*.

Among these defecations, dung beetles were present at two of 12 defecations (16.66%). I collected six defecations from the ground, either on leaf litter or exposed soil (50%), four from splatters on leaves (33.33%) and two were on a combination of leaves and the ground (16.66%). The mean weight of defecations was 30.49 g, the mean number of seeds present was 48.5, and the mean density of seeds was 2.17 seeds/g. See Table 2.
Sleeping Trees

I identified six sleeping trees. Of these, I identified the families of three trees. Two trees were Myristicaceae and one was a *Ficus* (family Moraceae). The mean DBH was 86.52 cm. None of the trees were fruiting. Dung beetles were present only underneath sleeping tree 3 (see Table 3). Research is limited on how howler monkeys choose their sleeping trees, but they generally prefer mature trees (Barbisan Fortes et al. 2013). The DBH I observed in this study is consistent with previous findings, and suggests that this group may prefer to sleep in mature trees. The mean tree crown diameter was 14.83 m, providing additional evidence that these were mature trees.

Table 2. Defecations and characteristics.

<table>
<thead>
<tr>
<th>Defecation</th>
<th>Weight (g)</th>
<th>seeds</th>
<th>seeds/g</th>
</tr>
</thead>
<tbody>
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<td>2.11</td>
<td>280</td>
<td>1.33</td>
</tr>
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<td>2</td>
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<td>3</td>
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<td>12.30</td>
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<td>15.60</td>
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<tr>
<td>7</td>
<td>8.30</td>
<td>9</td>
<td>1.08</td>
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<tr>
<td>8</td>
<td>11.80</td>
<td>8</td>
<td>0.68</td>
</tr>
<tr>
<td>9</td>
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<td>8</td>
<td>0.79</td>
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<td>10</td>
<td>11.50</td>
<td>109</td>
<td>9.48</td>
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<tr>
<td>11</td>
<td>14.10</td>
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</tr>
<tr>
<td>12</td>
<td>11.76</td>
<td>25</td>
<td>2.13</td>
</tr>
</tbody>
</table>

Mean weight: 30.49
Mean seeds: 48.50
Mean seeds/g: 2.17
Natural History Observations

The forest patch owned by ITEC is approximately 60 ha and is surrounded on two sides by cattle grazing land and is somewhat connected to two other forest fragments by low, brushy patches and some secondary forest. Despite its small size, I estimated that four howler groups live in the patch, with possibly a fifth group near enough to hear on some mornings, but I did not observe them in this forest patch over the summer. Also present was one group of white-faced capuchins (*Cebus capucinus*), with a minimum of 10 individuals including at least three infants. They move quickly and seemingly constantly through the forest understory and canopy. I observed them while following the howlers once per week. Typically, the howlers would be resting in the canopy while the capuchins travelled below them in the understory. I never observed members of the two groups interact. Through personal communication with local landowners I learned that some people have observed the capuchins displace the howlers from fruiting trees, which may be a more common occurrence during the times of year when fruit is more limited. This forest is profoundly wet, with a mean rainfall of

<table>
<thead>
<tr>
<th>Sleeping tree</th>
<th>Family</th>
<th>DBH (cm)</th>
<th>Fruiting (yes/no)</th>
<th>Dung Beetles (yes/no)</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>Myristicaceae</td>
<td>62.70</td>
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<td>no</td>
</tr>
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<td>no</td>
</tr>
<tr>
<td>3</td>
<td>Myristicaceae</td>
<td>46.15</td>
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<td>yes</td>
</tr>
<tr>
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<td>unknown</td>
<td>62.25</td>
<td>no</td>
<td>no</td>
</tr>
<tr>
<td>5</td>
<td><em>Ficus</em></td>
<td>175.70</td>
<td>no</td>
<td>no</td>
</tr>
<tr>
<td>6</td>
<td>unknown</td>
<td>107.91</td>
<td>no</td>
<td>no</td>
</tr>
</tbody>
</table>
14.7mm per day, with precipitation 22 out of the 30 days I recorded rainfall and 329 mm of rainfall total. July is one of the rainiest months on the island, but compared to other tropical forests, it is remarkably free of seasons, and July 2016 was actually slightly drier than the past 30-year average (Paton, 2015). I predict that fruit abundance was high during this time of year, and that the howlers were eating more fruit than is usual according to the literature.

I observed almost no social interactions between the howler monkeys within the group I followed. There was a young juvenile monkey who was very active compared to the surrounding adults. He or she ran on the branches and touched the adults, particularly one large adult male, and ran away while the slow adults tried to hit him or her in return. The juvenile would engage in this type of play on three occasions that I observed. He or she also was not as skilled at jumping from branch to branch as the adults, and on one occasion fell several feet before managing to grab onto a vine with his or her feet, hands, and tail and climb back up to the adults. On one occasion I observed two male howlers approach one another on a vine connecting two trees that was thick enough to walk and sit on, but not thick enough to pass another monkey. The males approached each other and when they met on the branch they extended their hands and grasped the other’s hand before passing each other clumsily on the vine and moving on. In general, the females were more difficult to find on any given day. They were more likely sitting closer to tree trunks or in dense foliage, while the males tended to be
on the edges of trees or on top of tree canopies. Perhaps these more exposed
vantage points are better for howling or vigilance.

I witnessed a confrontation between two howler groups once, when the
group I was following met another group that I dubbed the swamp group, due to
their apparent range in the lowest and swampiest part of the forest. The two
groups faced one another in the canopy and howled for approximately 30 minutes.
Females and males both howled, and there was quite a lot of movement, but I
could not tell who exactly was moving to where because I did not identify
individuals. After the bout I collected 12 g of feces. This was consistent with
Julliot’s observations that only ~60% of defecations occur in the sleeping areas,
and the remaining 40% occur on the edges of territories due to bouts like these
(Julliot 1997).

Non-primate species were also present at this site. Birds I encountered on a
daily basis included: Montezuma oropendola (*Psarocolius montezuma*), Northern
jacana (*Jacana spinosa*), Southern lapwing (*Vanellus chilensis*), black vulture
(*Coragyps atratus*), common black hawk (*Buteogallus anthracinus*) (a possible
predator for juvenile howlers), roadside hawk (*Rupornis magnirostris*), keel billed
toucan (*Rhamphastos sulfuratus*), red lored parrot (*Amazona autumnalis*), mealy
parrot (*Amazona farinosa*), great kiskadee (*Pitangus sulphuratus*), golden-
collared manakin (*Manacus vitellinus*), stripe throated hermit (*Phaethornis
striigularis*) and many others that I encountered less frequently. Other species I
encountered daily or almost daily included: fer-de-lance (*Bothrops asper*), vine
snake (*Oxybelus aeneus*), cane toad (*Bufo marinus*), strawberry poison frog (*Dendrobates pumilio*), red eyed tree frog (*Agalychnis callidryas*), brown throated three toed sloth (*Bradypus variegatus*), and Hoffman’s two toed sloth (*Choloepus hoffmanni*) and other herpetofauna and mammals encountered less frequently. The forest was also home to many rats and bats too numerous for me to properly identify. The island was devoid of any large bodied carnivores such as ocelots, jaguars, and harpy eagles, all species who are howler monkey predators when present. Their absence may contribute to the apparent success of the howlers in this patch.
CHAPTER V

DISCUSSION

I found differences in the abundance, species richness, Shannon-Wiener diversity, or Gini-Simpson diversity between the seedlings present underneath howler monkey sleeping trees and control areas. There is evidence to suggest that seeds underneath howler monkey sleeping trees arrived there via ingestion and defecation by the monkeys (Julliot, 1997; Pouvelle, et al. 2009; Anzures-Dadda et al. 2011), and this study suggests there is evidence that the presence or absence of this monkey group had an impact on the seedlings on the forest floor. These results are consistent with the results of Julliot (1992 & 1997), who found greater seedling abundance underneath howler sleeping trees, and with the results of Pouvelle (2009), who found increased abundance and diversity of seeds in the soil underneath red howler monkey sleeping sites in French Guiana. However, my results were not statistically significant, therefore a conclusion about this howler group’s effects on the seedling community cannot be made. Here I will offer some possible explanations for each of these results.

Seedling Diversity

I collected feces and counted the seeds within to connect some of the species the monkeys consumed with the seedlings underneath their sleeping trees, but identifying seeds in the field remained an obstacle to this objective. The most dominant seed present in the dung was a species of Ficus. The most compelling
seedling was unidentified, S42, of which I found 234 individual seedlings exclusively in transect 9, underneath sleeping tree 5 (which was an unidentified species of *Ficus*), but not in the control transect. They may have been deposited there as a result of endozoochory by the howlers, but that is far from the only possible explanation. Another explanation is that they are the offspring of the sleeping tree. Yet another is that they were deposited there by a secondary disperser, or by other animals that live in or interact with the tree, such as birds or *Ficus* consuming mammals. However, high concentration clumping of specific seed species is characteristic of howler seed dispersal patterns (Bravo, 2011) (but also kinkajou (*Potos flavus*) dispersal (Howe, et al. 1985)), and is not characteristic of birds and bats, whose in-flight defecations lead to a more uniform seed dispersal (birds: Bongers, 2001; Howe, et al. 1985; Gomes, Quirino, & Araujo, 2014; bats: Henry & Jouard, 2007). Clumping is also not characteristic of sympatric white-faced capuchin monkeys, who have a more scattered defecation pattern (Wehncke, Valdez, & Dominguez, 2003).

I found 12 seedling species found only underneath howler sleeping trees. S42, unidentified, was the most abundant, but a few others are worth exploring the likelihood that they were deposited there by howler defecation. I found 85 seedlings of an unidentified species in the genus *Psychotria* was found underneath sleeping trees, with only one underneath the control transects. *Psychotria* is a large genus in the Rubiaceae family (the Smithsonian Tropical Research Institute (STRI) lists 113 species in Panama). Most are woody shrubs and understory trees
with seeds between 5mm-1cm (medium seeds). It is difficult to draw conclusions about howler dispersal based only on this genus, because while howlers do eat the fruits of Rubiaceae and *Psychotria* (three species: Dias & Rangel-Negrín, 2013), this family and genus are not in the top four families and genera that comprise 36% of the howler diet: Moraceae, Fabaceae, Lauraceae, and Sapotaceae (Dias & Rangel-Negrín, 2013). Howlers prefer fruit from tall trees in the canopy rather than understory trees and shrubs (Dias & Rangel-Negrín, 2013). It is therefore unlikely that this clump of *Psychotria* seedlings was the result of howler endozoochory. The other Rubiaceae I found exclusively under sleeping trees were 11 individuals from one of two species in genus *Randia*. STRI lists 28 species of Panamanian *Randia*, and like *Psychotria*, it is a woody shrub or small tree, thus not a candidate for a howler’s favorite fruit.

Even more tenuous, because there were fewer individuals, 12 seedlings from genus *Annona* were present underneath the first sleeping tree. The crown of this tree was leaning over a cow pasture, so these seedlings were not in the forest but in a grass pasture filled with cattle manure and low canopy cover (<40%). This would be an ideal location for pioneer species that colonize canopy gaps and forest edges; however, there is little evidence that *Annona* are pioneer species, so their location in the pasture may not ultimately be a site of successful recruitment for the plants that arrived there. STRI lists 15 *Annona* species collected in Panama, of which howlers have been documented consuming four (Dias & Rangel-Negrín, 2013). Again, the clumping pattern is characteristic of mammal
dispersal, but with so few individuals present I cannot confirm that howlers deposited these seeds.

The remaining two morphotypes I found only underneath howler sleeping trees were *Eugenia* (family Myrtaceae, 7 individuals), and *Virola nobilis* (family Myristicaceae, 5 individuals). *Virola nobilis* were split between two sleeping trees with few individuals, which does not follow the characteristic clumping pattern of howler seed dispersal. It is worth noting, however, that the seeds of *Virola nobilis* are very large (> 2 cm long; Howe et al., 1985; personal observation). These large-seeded trees are more likely to rely on large-bodied mammals to disperse (Howe et al., 1985), and in the absence of spider monkeys (as is the case in this forest), howler monkeys and kinkajous (*Potos flavus*) may be among the only dispersers for this species.

Conversely, I found some morphotypes only in control areas. Four of these were unidentified, and in one unidentified Sapindaceae, *Paullinia glomerulosa*, *Inga oerstediana*, *Ficus urostigma*, and one unidentified Moraceae, only one individual was present. This leaves *Forsteronia sp.*, 10 individuals in control areas only, and *Trichilia tuberculata*, 17 individuals exclusively in control areas. *Forsteronia sp.* is a liana that produces long, thin fruits that dangle from its vines in clumps (STRI Herbarium). This is not a particularly good candidate for vertebrate dispersers, who generally prefer fleshy fruits, although howlers are known to be flexible and eat many parts of plants – they are no means restricted to fleshy fruits (Dias & Rangel Negrín, 2013). However, I could not find a published
instance of howler consumption of *Foresteronia*. This evidence suggests that it is highly unlikely the *Foresteronia* was dispersed by this howler group. *Trichilia tuberculata* was also present only in the control areas, but unlike *Foresteronia*, is a good candidate for howler dispersal, as it produces large seeds surrounded by a bright-red, fruit (STRI Herbarium). Red is presumed to be a signal to animals that can perceive it, such as howler monkeys and birds that the fruit is edible (Jacobs, Neitz, Deegan, & Neitz, 2015). I did not find a published instance of howler monkeys consuming this species specifically, but it is possible that these seedlings were dispersed by vertebrates. Most of the identified seedlings produce fleshy fruits in maturity, which are presumed to be dispersed via endozoochory, so it is possible that howlers might disperse them (Gallagher & Leishman, 2012), even though for most there is not a definitive answer.

The species accumulation curves (Figures 3 & 4) show an estimate of how species richness, Shannon Wiener (SW) diversity, and Gini-Simpson (GS) diversity will increase as sample size increases. The extrapolation shows SW and GS diversity does not increase with more seedling samples for either sleeping or control transects, indicating that I can be confident I have calculated the true diversity indexes for those transects. Species richness, however, continues to climb with increased sampling. The curve flattens out at approximately 740 samples for both sleeping and control transects, but the extrapolation does increase beyond 1,000 samples.
Seedling Abundance

I found a greater number of seedlings underneath sleeping trees than in control plots, and although this difference was not significant ($p = .34$), it can be explained in a few ways. First, there may be differences in soil quality between the areas where the howlers defecate and the areas they do not. Nagy and Milton (1979) found evidence that howler dung has a higher concentration of nitrogen and phosphorus than either the feces of sympatric primates or leaf litter, and suggest that this makes howler feces highly nutritious for plants. This fecal nutrient surplus may be a result of their naturally poor nutritional intake during the digestion of leaves, which are the majority of their diet (Milton, 1980).

Whatever the reason, Feeley (2005) found that nutritional intake is higher in seeds fertilized by howler monkey dung, and that the soil in areas of consistent howler defecations (i.e., latrines) have a higher concentration of the highly effective fertilizers, nitrogen and phosphorous. This is likely to play a role in the higher germination rates found by Julliot (1992, 1997) and Bravo (2001). These higher germination rates persist despite evidence that the presence of dung attracts more seed-predating rodents (Anderson, 2002), and that seed clumping is not the most conducive microenvironment for seedling establishment (Howe & Smallwood, 1982; Anderson, 2002; Giraldo et al. 2007). The high nutritional value of howler dung, and consequently howler latrines, may cancel out any clumping or density-related seedling mortality.
The literature on the effects of secondary seed dispersers on howler monkey-defecated seeds is limited, but what evidence we have suggests that dung beetles and rodents do play a role in determining a seed’s ultimate destination. Anderson (2004) found that rodents kill seeds at significant rates, particularly when there is a high volume of feces in the defecation. These seeds are most likely doomed to death, either by predation or by being moved outside of a location suitable for establishment. She also found that dung beetles move seeds, particularly those surrounded by dung, but not very far (10-33 cm), showing that dung beetles do not move seeds outside of the suitable germination location, the latrine. Thus it is unlikely (but not impossible) that dung beetles moved seeds from the howler defecations outside the sleeping tree transects in my study. Following the activities of dung beetles and rodents the period after howler defecation would be a valuable future avenue of study in this forest going forward.

Feces

Conclusions about howler diet are difficult from such a small sample size ($n = 12$) combined with the large number of unknown seeds (509) within these fecal samples. For the 18 days of feces collection, *Ficus* was a dominant food source, whose seeds made up over half (52%) of all seeds present. Studies show that *Ficus* is a key genus for howler monkeys from Mexico to the Amazon (Amato & Estrada, 2010; Arroyo-Rodríguez et al. 2014; Bravo, 2011; Chapman,
1989; Estrada & Coates-Estrada, 1991; Julliot, 1997). They consume some part (ripe and unripe fruits, leaves, petioles) of 61 species of *Ficus* (Dias & Rangel-Negrín, 2013). *Ficus* trees are asynchronous, meaning they do not have a designated fruiting season, instead, individuals fruit at different times. It is likely that at any given time of year there is at least one fruiting *Ficus* in a howler troop’s range (Janzen, 1979).

I also identified a seed from *Spondias mombin*, which was fruiting robustly all over the forest during this observation period. *Spondias* seeds are very large (> 2 cm), and the presence of even one in howler dung is notable, because while many species may consume *Spondias* fruits, only the large-bodied animals can carry the seeds away from the parent tree, which is important for recruitment according to the Janzen-Connell hypothesis. In the absence of other large-bodied atelines, this may be only the howler monkey in this forest fragment. It is impossible to make any conclusive generalizations, but based on the seeds in the feces collected, the howlers in this forest may be important dispersers for *Ficus* and *Spondias mombin*. See Appendix B for photos of both *Ficus* and *Spondias mombin* seeds.

Some seed fragments were present in each defecation, evidence of seed predation by the howlers. I could not identify these seeds as one of the morphs and were not counted along with the intact seeds. Based on how few fragments were present compared to intact seeds, I think seed predation is minimal, although
studying the seed fragments found in the feces and better understanding what percentage of consumed seeds are killed could be an area of future investigation.
CHAPTER VI
CONCLUSION

I did not find significant differences in abundance, species richness, Shannon-Wiener diversity, or Simpson diversity between seedling populations underneath howler sleeping trees compared to control areas. These results are not consistent with others that investigate howler monkey seed dispersal (Julliot, 1997; Bravo, 2001). It is possible that, as this data suggests, the howlers do not have a significant impact on the forest floor seedling community, but I will address a few ways in which this study could be improved, and improvements may affect results.

First, I relied heavily on previous compilations of howler diet data to determine what fruits my study troop were likely to eat. Most long-term diet studies on Alouatta palliata occur in the dry forests of Southern Mexico and Costa Rica (44/54, 81%) (Dias & Rangel-Negrín, 2013). Not only do the flora species differ between Panama and Mexico (and to a lesser extent Costa Rica), but also these studies are located in seasonal dry forests. Fruit consumption in howlers is positively correlated with increased rainfall (Dias & Rangel-Negrín, 2013), and in a wet forest like the one on Isla Colón, it is likely that the fruit consumption patterns of Panamanian A. palliata are more similar to Alouatta species guariba, seniculus, and caraya, species that live in the wet Amazon. Diet studies are much more limited for these species, and due to the high beta diversity of tropical trees, it is unlikely that A. palliata is consuming precisely the same
species as its southern counterparts. A detailed, long-term study of what fruits the monkeys at this site consume would be highly valuable information for those interested in how howlers disperse seeds in this particular forest.

In this study, I identified and followed only one howler troop. The scope of the study would be broadened by simply following another group for the same amount of time, identifying their sleeping trees, and assessing if the results were consistent. Greater sample size in transects and feces collection would provide a more complete picture of the howlers’ ecological role. Data collected across seasons or over the course of several years would be even more ideal to control for seasonal factors. This study examines the howlers in their environment in a narrow window of time.

I relied on past studies that definitively show that howlers use the same sleeping trees repeatedly, but ideally, one would follow a group for a longer amount of time to determine the group’s true range, and determine what sleeping trees they frequent the most often. I assumed that the trees I found the howlers in had been used before based on previous literature, but it is impossible to know how much the groups on Isla Colón differ from the literature in this respect, if at all.

Of course, this study was limited by tropical seed identification, and to a lesser extent, seedlings and trees. I relied heavily on ecologists and botanists at the field site, and a few key literature resources, but a more reliable plan for plant
identification will be essential for anyone interested in the complex relationship between plants and animals.

This study provides important data about the composition of seedlings and the dietary and spatial habits of one of the howler monkey groups at this site.

Additional studies of monkeys in the Bocas del Toro region are needed, and urgently, as already fragmented forests shrink and separate. Howler monkeys are perhaps better suited to tolerate some of these changes than monkeys with larger home ranges and more specific nutritional needs, but they are not immune to all the negative effects of a dwindling forest canopy and increased human activity. As these human activities increase, we may see a decline in other large-bodied mammals where the howler monkeys can still persist, which makes this species an important one for ecologists and conservationists to understand. The howler population in the Bocas del Toro region is little studied, and is in a different ecological niche than its conspecifics in dry forests, but has greater anthropocentric pressures than its conspecifics on Barro Colorado Island. This study may be a starting point for future researchers interested in seed dispersal, herbivore ecology, and the ecology of increasingly fragmented rainforests. These results may be a small contribution to our knowledge of just one of the many howler groups in the region, but will hopefully lead to more research.

The monkeys on these islands are uniquely situated to be ambassadors to the rainforest for the many visitors that pass through their territories. The sounds of howlers roaring at daybreak is one that stays with tourists as a quintessential
memory from the Neotropics. By understanding their environmental needs and contributions more thoroughly, we can ensure that humans remain enchanted by these remarkable monkeys and their healthy forest homes well into the future.
REFERENCES


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APPENDIX A

Howler monkeys in study group
APPENDIX B

Seeds from howler monkey defecation *Spondias mombin* (Seed 6) and *Ficus* (Seed 2)
APPENDIX C

Seedling 18 (*Virola nobilis*) and many seedlings
APPENDIX D

Seedling 34 (*Callychlamys latifolia*) and Seedling 30 (*Paullina mallphylla*)