THE ROLE OF RODENTS IN TROPICAL FOREST REGENERATION: SEED PREDATION AND SEED DISPERSAL

By Jacob W. Dittel

Small rodents have long been considered to be seed predators rather than effective seed dispersers. Particularly in the Neotropics, this predatory role has been thought to be especially true for large-seeded plant species that likely had mutualistic relationships with megafauna that went extinct after the last ice age. Small rodents are not thought to be dispersers because they presumably eat a large proportion of the seeds or cannot move the large seeds sufficiently far to be effective dispersers. In this study, I tracked the removal of seeds from three different heights of three species of large-seeded trees in central Panama, *Attalea butyracea, Astrocaryum standleyanum,* and *Dipteryx oleifera*, and followed the removed seeds to deposition sites in central Panama. Removals were most likely perpetrated by two small rodents, the strictly terrestrial *Proechimys semispinosus* (Central American spiny rat) and the arboreal *Sciurus granatensis* (red-tailed squirrel) because they were the most abundant small rodents in the study sites. At each deposition site, I measured 9 microhabitat variables to determine if these two rodents were preferentially depositing seeds at sites with certain characteristics or were randomly depositing seeds. During my study, rodents handled 98 seeds; 12 seeds were taken into subterranean burrows or into the canopy and therefore unlikely to successfully recruit, while only one seed was preyed upon. On average, *A. butyracea* was moved 6.5 m before being deposited. *Astrocaryum standleyanum* had an average distance moved of 1.4 m. In all cases, seeds were most likely to be deposited with the fruit eaten, but the seed remained intact. Additionally, rodents deposited seeds in locations with large logs (> 10cm diameter), high herbaceous cover, and an intact canopy. The number of large logs was significantly different from random locations. Despite not being able to determine long-term fate (greater than ca. 1 year), I show that these small rodents are not primarily seed predators and may in fact be important mutualists by dispersing seeds relatively long distances to favorable germination sites.

THE ROLE OF RODENTS IN TROPICAL FOREST REGENERATION:
SEED PREDATION AND SEED DISPERSAL

By

Jacob W. Dittel

A Thesis Submitted
In Partial Fulfillment of the Requirements
For the Degree of

Master of Science – Biology

Biology

At

The University of Wisconsin Oshkosh
Oshkosh WI 54901-8621

May 2014

COMMITTEE APPROVAL

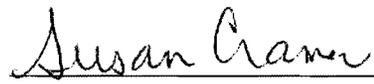_____ Advisor

15 MAY 2014 Date Approved

_____ Member

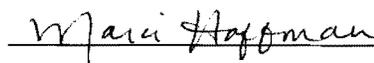_5 / 15 / 2014_ Date Approved

_____ Member

_____ Member

_5/15/2014_ Date Approved

DEAN OF GRADUATE STUDIES

_____

_5/15/2014_
Date Approved

FORMAT APPROVAL

_____

_4/24/14_
Date Approved

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

Chapter I

Introduction

Seed dispersal represents one of the most critical stages in the life history of plants (Terborgh1970). Dispersal is necessary for plants to colonize disturbed regions, avoid competition and predation, and locate suitable microhabitats for germination and subsequent growth (Howe & Smallwood 1982). Plants can disperse their seeds biotically or abiotically and have evolved a great number of modifications to their seeds to aid in dispersal. Traits include fleshy fruits, chemicals, and bright colors to lure animals to their seeds and in return having their seeds dispersed intentionally or unintentionally. Plants have also evolved seeds with high surface area (creating wings), low density, and reduced size to utilize abiotic mechanisms such as wind, gravity, and water. There are typically stark differences between seeds with "reduced" morphologies for abiotic dispersal compared to seeds with large, succulent, and colorful fruits for biotic dispersal.

There are three main hypotheses as to why seed dispersal evolved in plants: the escape hypothesis, colonization hypothesis, and directed dispersal hypothesis. None of these hypotheses are mutually exclusive and are probably all a factor in the need to disperse seeds (Howe & Smallwood 1982). The escape hypothesis states that seeds that are displaced from parent plants have an increased chance of survival. This relationship between dispersal distance and seed survival is often referred to as the Janzen-Connell model (Janzen 1970; Connell 1971). High densities of seeds found under parent plants act as "magnets" to seed predators and pathogens, which in turn focus their attention beneath

the parent plant, often ignoring seeds that are only a few meters away from the parent

(Janzen 1970). Therefore, according to the Janzen-Connell model, seeds found near

parent plants in high densities should have almost no chance of survival, while seeds that

are displaced from the parent plants and siblings should have a greater chance of survival

the farther they are displaced from the parent plant (usually on the order of tens of

meters) and the less densely they are found (Clark & Clark 1984).

The colonization hypothesis assumes that habitats are constantly changing, and

the current habitat that a parent plant inhabits may not be currently suitable for seed and

seedling survival. Therefore, plants disperse seeds over space and time to ensure that

some of their seeds will encounter a favorable habitat or are able to wait until the location

at which they fall becomes favorable (Howe & Smallwood 1982). Many plants

accomplish this by producing seeds that can lie dormant for many years. Habitats could

become favorable and promote seed growth after disturbances such as tree falls and fires.

The directed dispersal hypothesis argues that plants have evolved seed adaptations

to increase the probability that seeds will reach sites suitable for germination (Howe &

Smallwood 1982; Howe 1986). Directed dispersal suggests that animals non-randomly

disperse seeds into locations that favor seed germination. This hypothesis best explains

animal-mediated dispersal. Seed adaptations therefore evolved in response to mutualistic

relationships formed with animals that would non-randomly cache or deposit seeds in

locations that would favor seed development.

None of the three proposed hypotheses can adequately explain seed dispersal, in

large part because the reason needed for seed dispersal may differ among plant

populations (Howe & Smallwood 1982). The validity of these hypotheses is often criticized due to a lack of supporting evidence or to conflicting results of studies that support and refute a single hypothesis. Another reason for the lack of an exclusive hypothesis is the long life spans of large plants, which renders some hypotheses such as the colonization hypothesis difficult or nearly impossible to test. Seeds could lay dormant for years while awaiting proper conditions to germinate. Studies of sufficient duration would be logistically infeasible, and there is no guarantee that studied seeds would fall in a location that will at some time become habitable. Finally, each hypothesis alone may not place sufficient emphasis on selective pressures on plants alone to direct the evolution of dispersal. It may require a combination of hypotheses to explain plant adaptations for seed dispersal.

Chapter II

Directed Seed Dispersal by Rodents

In a Lowland Forest in Central Panama

Introduction

Tropical forests arguably are Earth's most species-rich ecosystems, and therefore it can be presumed that seed dispersal mechanisms are correspondingly diverse (Terborgh 1970). Small rodents, owing to their diversity, ubiquity, and abundance throughout most tropical forests, typically remove vast numbers of seeds in tropical forests. However, such rodents have generally been considered seed predators rather than dispersal agents (Hume 1994; Vandermeer 1979; Terborgh *et al.* 1993; but see Vander Wall *et al.* 2005). This supposition is based on the premise that small rodents primarily predate seeds and do not or rarely disperse seeds, thereby having an overall negative effect on plant survivorship and recruitment. However, recent work has shown that rodents previously thought to be solely seed predators are in fact also important seed dispersers (Forget 1991a; Hoch & Adler 1997; Adler & Kestell 1998; Carvajal & Adler 2008; Kilgore *et al.* 2010; Jansen *et al.* 2012; Lambert *et al.* 2014).

In central Panama, two presumably important rodent dispersers of seeds are the terrestrial spiny rat (*Proechimys semispinosus*) and the arboreal red-tailed squirrel (*Sciurus granatensis*). *Proechimys semispinosus* is the most abundant rodent in many lowland tropical forests, and *S. granatensis* is overwhelmingly the most abundant sciurid in such forests. Both species have a generalized diet that includes both the fruits and

seeds of most tropical trees, typically preferring large-seeded species (Adler 1995; Glanz 1984).

Despite the ubiquity of *P. semispinosus* throughout lowland tropical forests within its geographical distribution, it is associated with second-growth forests, particularly recently disturbed areas such as tree-fall gaps (Tomblin & Adler 1998; Lambert & Adler 2000; Adler 2000). *Sciurus granatensis* is associated with palm stands (Glanz 1984), particularly those species of palms that are light demanding and thereby associated with second-growth forests. Both species scatter-hoard seeds (Hoch & Adler 1997; Adler & Kestell 1998; Kilgore *et al.* 2010; Carvajal & Adler 2008; Heaney & Thorington 1978), and their habitat associations and scatter-hoarding proclivities could have major impacts on tropical plant distributions (Carvajal & Adler 2008).

Previous studies have examined seed dispersal by these two rodents but did not address long-term seed fate. Carvajal and Adler (2008) studied seed removal differences and short-term fates between tree-fall gaps and intact forest in relation to habitat associations of the two species. *Proechimys semispinosus* was more abundant in tree-fall gaps and removed more seeds from such gaps. By contrast, *S. granatensis* was more frequently observed in intact forest and correspondingly removed more seeds from such forest. This study was noteworthy because not only did *P. semispinosus* and *S. granatensis* remove seeds, but they did indeed scatter-hoard them. Rodents that bury seeds under leaf litter and into the soil often increase plant fitness by decreasing the probability of desiccation, thereby facilitating germination and rooting and reducing predation (Forget 1991a, b; Forget et al. 1994; Forget & Milleron 1991).

Flagel *et al*. (2009) examined the influence of seed height on the rate of removal. They placed semi-permeable exclosures at three different heights (ground, sub-canopy, and canopy) and recorded removal of *Astrocaryum standleyanum* and *Attalea butyracea* seeds. Most seeds were removed from ground level and were assumed to be most likely removed by *P. semispinosus* because that species was the most abundant terrestrial rodent in the study area (Flagel *et al*. 2009). *Sciurus granatensis* also removed a small proportion of seeds and carried them into the canopy or cached them in the ground based upon results Carvajal and Adler (2008). The sub-canopy and canopy seeds were most likely solely removed by red-tailed squirrels because they were the most common arboreal rodent and were the only observed such rodent sufficiently robust to carry the fruits that were used in the experiment (Flagel *et al.* 2009). That study showed that fruit removal does not only occur after the fruit has fallen but that ripe fruit may be removed while still in the tree, thereby necessitating the study of all phases of a seed's life.

Scatter-hoarding may be detrimental if rodents cache seeds in locations where they cannot germinate. Therefore, it is also important to follow seed removal to deposition site to quantify the relationship that rodents have with plants. Carvajal and Adler (2008) examined two gross habitat types (tree-fall gap vs. intact forest) and showed that more seeds of *A. butyracea* and were moved into gaps than understory. *Proechimys semispinosus* moved almost twice as many seeds into gaps, while *S. granatensis* cached a majority of seeds in intact forest; corresponding with preferred habitats of both species (Carvajal & Adler 2008). This dispersal patterns is important for *A. butyracea* because it is a light-demanding species (Araus & Hogan 1994; Hogan 1988), and being dispersed

into gaps may proffer an advantage. Kilgore *et al.* (2010) examine microhabitat of seed deposition of both *A. standleyanum and A. butyracea*. They found that seeds were more likely to be placed in areas of denser canopies with more lianas. The difference in seed cache location between Kilgore *et al.* (2010) and Carvajal and Adler (2008) was attributed to differences in forest age between the two study sites. Dispersal into liana tangles are likely still beneficial to these palms because rodents are moving them away from conspecifics, thereby reducing Janzen-Connell effects (Kilgore *et al.* 2010*; but see* Harms & Dalling 2000; Wright 1983) and potentially reducing subsequent predation, thereby allowing the seeds to remain dormant undisturbed until conditions conducive to germination are met. Additionally lianas are associated with tree gaps (Laurance *et al.* 2001) so seeds of light-demanding species are likely to be more successfully in liana tangles.

Unfortunately, the extent to which these two common and widely-distributed rodents influence long-term seed fate is poorly known. Such information is sorely needed, given the ubiquity, abundance, and presumed importance of such rodents in influencing seed fates. Accordingly, my aim was to incorporate three phases (seed height, microhabitat of deposition site, and fate) of seed removal by *P. semispinosus* and *S. granatensis* into one study.

Methods

     Study area.

     The study was conducted in Soberanía National Park in central Panama near the town of Gamboa (9°10'N, 79°45'W) from near the beginning of Pipeline Road to just north of Rio Juan Grande (i.e., the first 7 km along the road). Soberanía National Park is a 22,000-ha park containing tropical moist forest. The park has second-growth forest of varying ages, with scattered patches of old growth forest, and ranges in elevation from 30 to 200 m (Karr 1990). The annual rainfall is approximately 2612 mm, based on the nearest meteorological station to the study area (Barro Colorado Island; Windsor, 1990). Soberanía National Park experiences seasonal precipitation, with a dry season generally occurring from the end of December through the end of April, followed by a rainy season during which approximately 90% of precipitation occurs. Pipeline Road is an unimproved dirt track that runs southeast to northwest through the park and allows access to the forest.

     Along Pipeline Road, six study sites, measuring 100 m wide by 180 m long, were randomly selected, three on each side of the road (east and west). Each study site contained three lines (designated A, B, and C) marked at 0, 50, and 100 m. Each line contained ten sampling stations (1-10) spaced at 20-m intervals.

     Study organisms.

Three common species of trees in Soberanía National Park, including the palms *Astrocaryum standleyanum* L.H. Bailey and *Attalea butyracea* (Mutis ex L.F.) Wess.

Boer and the large canopy tree *Dipteryx oleifera* Benth, were included in the study. Both

species of palms produce large fruits (ca. 4 cm × 3 cm for *A. standleyanum* and 6 cm × 3

cm for *A. butyracea*) during the rainy season. The fruits generally contain a single seed.

Fruits and seeds of both species are important food sources for rodents (Adler 1998;

Carvajal & Adler 2008). *Dipteryx oleifera* is a large-seeded member of the family

Fabaceae. Fruits are approximately 6 cm × 2.5 cm and contain single seeds. Unlike most

fruiting plants in central Panama, this tree fruits near the beginning of the dry season,

making it one of the only large fruits available to rodents during this time of the year

(Carvajal & Adler 2008). The fruits of all three species have fleshy mesocarps and stony

endocarps that protect the seeds. Rodents consume both the fleshy mesocarps and seed

contents (Adler 1995; Glanz *et al.* 1982)

     Proechimys semispinosus (Central American spiny rat) and *Sciurus granatensis*

(red-tailed squirrel) were focused upon in this study based on their abundance within the

study site (Kilgore *et al*. 2010) and potential importance in seed removal (Carvajal &

Adler 2008). The strictly-terrestrial *P. semispinosus* consumes and sometimes scatter-

hoards and larder-hoards a wide variety of seeds (Adler 1995; Adler & Kestell 1998;

Hoch & Adler 1997). *Sciurus granatensis* is mostly arboreal but frequently forages on the

ground and sometimes scatter hoards seeds on the ground. However, *S. granatensis* also

caches seeds in trees (Heaney & Thorington 1978; Carvajal & Adler 2008). Larder-

hoarding, where animals create few large caches and primarily in underground burrows

by *P. semispinosus* and in trees by *S. granatensis,* presumably leads to seed death

(Carvajal & Adler 2008) because the seeds are either buried too deep to germinate or are permanently stored in trees until consumption.

Rodent sampling.

Spiny rat abundance was determined by live trapping on the six study sites. One Tomahawk live-trap (40.5 × 12.6 × 13 cm, Tomahawk, Wisconsin, USA) was placed at each station within a study site, forming a 3 × 10 grid. Traps were set on the ground and baited with cut ripe plantain covered with vanilla extract. Traps were set for 10 consecutive nights and checked each morning. Captured rodents were ear-tagged with a small, serially numbered metal tag (National Band and Tag Company, Newport, Kentucky, USA), weighed, aged (juvenile, subadult, or adult, based upon pelage; Adler, 1994), and sexed before release at their respective capture locations. Sampling was conducted one time at the beginning of each field season (late May during the rainy season and early January in the dry season).

Red-tailed squirrels are difficult to sample by live trapping (Carvajal & Adler 2008). To estimate relative abundance, sight surveys were performed by walking within a study site along each transect. Visual surveys were complemented by stopping at stations 2, 5, and 8 on the B line and sitting quietly for 20 minutes. Sight surveys were conducted at each study site once per week during each field season.

Fruit availability.

Fruit availability was estimated by walking each study site along the transects. All ripe fruits known to be eaten by the study rodents (Adler 1995; Glanz 1984) observed within 5 m of the transect, either in a tree or on the ground, were recorded and identified to species, and each individual tree producing such fruit was counted as a single observation. Fruit availability was determined three times during the rainy (before, during, and after experimentation) and twice in the dry season (before and after experimentation).

Fruit removal and tracking.

During the rainy season, both palm seed species were placed sequentially within the study sites for 20 days each, whereby their removal rates and cache locations were recorded. During the dry season, only seeds of D. oleifera were placed in exclosures. Each seed had a small hole (<3 mm in diameter) drilled at the opposite end of the cotyledon in an attempt to not kill the embryo. Annealed wire (22 gauge) was passed through the hole with an approximately 2-mm tail, and an industrial sewing bobbin (Style 7 cocoon bobbins, Middleburg Threads Inc., Allentown, Pa, USA) was attached to the seed via the wire. The bobbins were wrapped in white waterproof fabric tape to prevent unintended unraveling and to secure the bobbin to the wire. The bobbins contained approximately 91 m of thread, which was much greater than the predicted distance that seeds would travel. Five seeds with fresh ripe mesocarps were placed in Tomahawk live traps that were wired open. These semi-permeable seed exclosures allowed smaller

rodents access to the seeds but omitted larger mammals (typically >800 g). The loose end of the bobbin thread was tied to the seed exclosure such that the thread could be followed to final seed placement. Nine seed exclosures were placed within each study site along the B line at station 2, midway between stations 5 and 6 (5.5), and at station 8. Three seed exclosures were placed at varying heights at each station. Exclosures were placed on the ground (0 m), in the sub-canopy (up to 5 m above ground), and in the canopy (> 5 m above ground). Exclosures at the sub-canopy level were affixed to lianas or tree branches with bungee cords, while exclosures in the canopy were raised by rope until they rested securely against a large tree branch or liana so that rodents traveling through the canopy could readily enter the exclosure (see Lambert *et al.* 2005; Kilgore et al. 2010; Flagel et al. 2009).

Five fruits from a single species were placed within the exclosures for 20 days. Fruits of *A. standleyanum*, followed by those of *A. butyracea*, were used during the rainy season for a total of 40 days, and fruits of *D. oleifera* were used during the dry season for 20 days. Seed exclosures were checked daily, and fruits that were removed, eaten in the exclosure, or rotten were replaced with fresh fruit. All deposition locations were marked with a pin flag.

Microhabitat associations and seed fates.

All fruits that were removed from the exclosures were found by following the thread from the bobbins. For seeds that could be located, the linear distance moved and direction from the exclosure was recorded. Nine different microhabitat variables in five

quadrants (for a total of 45 measurements) were measured at each exclosure, each seed

deposition site, and a randomly-selected location (Table 1). Random locations were

determined by randomly selecting a compass direction and moving the same distance to

which a seed was moved from the exclosure. The densiometer was a small

(approximately 10 cm) convex mirror with a 1 cm × 1cm grid etched into it. The density

was calculated by taking the mean number of squares with at least 50% open sky

recorded at the end of a 6-m rope that extended in each cardinal direction from the center.

Data collection for the other variables are explained in Table 1.

Once seeds were located, their fates were determined. Seeds could either be

untouched, fruit eaten and seed intact in the exclosure, fruit and seed eaten within the

exclosure, or fruit and seed removed from the exclosure. All removed fruits that could be

found were classified as fruit and seed intact, fruit eaten and seed intact, both fruit and

seed eaten, or seed taken into a subterranean burrow or into a tree (and therefore

presumably dead). All fruits that were removed but could not be found were designated

as fruit removed and seed fate unknown and excluded from further fate analysis. For each

removed fruit that was located, the thread was detached from the exclosure and

reattached to a nearby plant to allow the tracking of any potential future movements.

Seed locations were marked with pin flags, and the seed fates were monitored daily. All

removed seeds were subsequently assigned to the same fate categories as the seeds from

the exclosures. If the fruit and seed were moved again, the event was considered to

represent secondary dispersal. If upon further removal events in which the seed remained

intact, microhabitat data at the seed's new location were recorded. If multiple seeds were

cached in a single location, only one microhabitat data point was measured to avoid problems associated with independence. Pin flags were left in place between field seasons in hopes of finding scatter-hoarded seeds and establishing long-term fates. If such seeds were found, then their fate was recorded as previously described.

Data analysis.

Rodent abundance (*P. semispinosus*, *S. granatensis*, and both combined) and fruit availability, all recorded as counts, were analyzed by constructing full log linear models that included plot and year as main effects and the plot x year interaction. I compared mean distances that seeds were moved from the exclosures by species (*A. standleyanum* and *A butyracea*) and year with t-tests. Microhabitat data were analyzed using backward elimination three-group discriminant function analysis to search for patterns in the distribution of seed caches. Exclosure locations, seed caches, and random locations composed the three groups. Variables that were retained in the model were then analyzed using analysis of variance to determine if that variable was unique to the seed cache site or if it was a ubiquitous characteristic shared with the random location and seed-exclosure station. All microhabitat data of fruit cache sites were omitted if the seed was moved from the seed exclosure station less than 5 m to eliminate the problem of independence. Distances that seeds each seed species were moved were compared to each other using t-tests. Distributions of seeds in fate categories were compared using log-linear analysis. Seed fate categories were fruit and seed intact, fruit eaten seed intact, and seed predated (seed eaten or seed taken into subterranean burrow or canopy where it was

assumed to be predated). All data analysis was performed using SAS software (Version 9.3, SAS Institute Inc.) and Program R (Version 3.1.0, R Foundation for Statistical Computing).

Results

I accumulated a total of 7,200 trap nights during rodent live-trapping. *Proechimys semispinosus* was the most frequently-captured rodent, with a total of 142 individuals being captured over the four sampling seasons. The only other species of rodents captured during the study period were two individual *Hoplomys gymnurus* (armored rat) and one individual *S. granatensis*. The two *H. gymnurus* individuals were each captured once during the rainy season of 2009 and during the dry season of 2010. The *S. granatensis* individual was captured multiple times during the dry season of 2011. I observed 28 *S. granatensis* during 40 hours of squirrel censuses. *Proechimys semispinosus* and *S. granatensis* were captured or observed on all plots at some point during the study period. Neither total rodent abundance nor squirrel abundance varied among plots (χ^2= 5.70, p=0.3365;χ^2= 4.14, p=0.5288, respectively), but *P. semispinosus* abundance did vary (χ^2=32.73, p=<0.0001). Plot 6 had the most *P. semispinosus*, while plot 2 had the fewest. *Proechimys semispinosus* also showed variance among sampling periods (χ^2=6.75, p=0.009), but no plot by period effect was observed (χ^2=3.08, p=0.0793). Total rodent abundance did not vary among plots or sampling periods (χ^2=0.05, p=0.8228; χ^2= 7.46, p=0.1889, respectively), nor was there a plot by period

interaction (χ^2=2.47, p=0.781). *Sciurus granatensis* abundance did not vary over plots (χ^2= 1.28, p=0.2571) or years (χ^2= 0.11, p=0.745), nor was there a plot by year interaction (χ^2= 6.65, p=0.2478).

Fruit availability was greater during the rainy seasons ($\bar{x}$ = 25.25 fruiting plants per plot) than during the dry seasons ($\bar{x}$ = 5.6 fruiting plants per plot). Availability differed among plots (χ^2=41.17, p = <0.001) but not years (χ^2= 1.06, p=0.3025). Plot 5 produced the most fruit, while plot 1 produced the least. However, there was an interaction between plot and year (χ^2= 14.46, p=0.0129).

In 27,000 fruit days (where one fruit day is equivalent to a single fruit available for 1 day, e.g. Flagel *et al.* 2009), rodents removed 97 seeds; 85 seeds were removed during the rainy seasons, and 12 additional seeds were removed during the 2010 dry season. Seed removal data were not available during the 2011 dry season because *D. oleifera* was not fruiting during the study period that year. Due to the small sample size of seed removal during the dry season, those data were included with the rainy season data, and seasonal differences were not investigated.

Most seeds removed during the rainy seasons were removed from the ground (55 seeds); 26 of the remaining seeds were removed from the sub canopy and 4 from the canopy. All subcanopy and canopy seeds were assumed to have been removed by *S. granatensis* because *P. semispinosus* is strictly terrestrial (Adler 2000). Only one other arboreal rodent, *Diplomys labilis* (rufous tree rat), is sufficiently large to transport palm seeds, but they are rare in the study area (Flagel *et. al.* 2009, personal observations). We could not identify the removal agents of seeds taken from ground exclosures unless the

seed was carried into trees; 5 such seeds removed from the ground were carried into the canopy and therefore most likely removed by *S. granatensis*. Most other such seeds likely were removed by *P. semispinosus* based on its abundance. Plot 1 experienced the most removals, while plot 6 had the fewest removals. There was an association between the number of seeds removed and abundance of all rodents (χ^2= 28.94, p=0.0003), abundance of *P. semispinosus* (χ^2= 23.75, p=0.0047), and of *S. granatensis* (χ^2= 25.60, p=<0.0001). Overall, plot had an effect on *P. semispinosus* abundance, fruit availability, and seed removal. Only *P. semispinosus* abundance was affected by year. Seed removal was also correlated with the abundance of all rodents (Table 2).

Most removed seeds that I recovered were placed on top of the leaf litter and were never buried in the soil. I also never found seeds that were completely covered with leaf litter, but some were pressed into the litter. Most seeds were cached individually, with only one cache having more than one seed; this cache contained four seeds. Twelve seeds experienced two movements; however only one of the 98 removed seeds experienced more than two movement events. After initially being moved 13 m, this seed was moved 14 m a second time and 6 m a third time. The seed remained intact throughout the study. Overall, seeds were moved a mean distance of 5.15 m from the exclosure. However, *A. butyracea* seeds were moved a mean of 6.50 m, while those of *A. standleyanum* were moved a mean of only 1.43 m. Furthermore, the longest movement of an *A. butyracea* seed was 42.6 m, while the longest movement of an *A. standleyanum* seed was only 7.5 m. There was a difference in distance moved between seed species (t=3.45, p=0.0013) but not between years (t= 1.35, p=0.184).

The distribution of distance and seed fate differed significantly (χ^2 = 67.66, p<0.0001). Most seeds were moved a short distance (< 3m) and were deposited with the fruit eaten but the seed left intact. The next greatest portion of seeds was moved a longer distance (>3m) and deposited with the fruit eaten but the seed intact. I was unable to determine longer-term fates of removed seeds because the industrial bobbins degraded after several months. A small sample (8%) of the removed seeds remained at their initial cache site until the end of the project (ca. 1.5 years). Of the *A. standleyanum* and *A. butyracea* seeds that were removed during the first season (50 seeds), 9 were still present to the dry season, and of those 9 seeds, 5 were present to the end of the project. Of the *D. oleifera* seeds that were removed (19), 4 seeds were present to the end of the project. However, the hole in the seeds exposed them to small predators and fungal growth. Such seeds did not germinate and were likely unpalatable to rodents before re-caching or consumption could occur.

Of the 98 seeds removed during the study, 28 were moved farther than 3 m from the exclosure and were undamaged and therefore retained for the microhabitat analysis; 22 seeds were removed and taken into a burrow (and assumed to have been destroyed), while 47 seeds were moved less than 3 m. Discriminant function analysis yielded a first canonical axis that explained 56% of the variance, while the second canonical axis explained 44% (Figure 2, Wilk's Lambda = 0.569, P = 0.0145). The number of logs (>10cm) was most closely associated with the first axis, while the distance to the nearest tree was most closely associated with the second axis. Canopy density and herbaceous cover also were strongly associated with the first axis, and tree diameter was associated

with axis 2. Group centroids (exclosure, cache, and random) strongly differed from one

another, and the standard error of the means did not overlap (Figure 2). Seed exclosure

locations were associated with distance from tree (axis 2, 90%). Because I intentionally

placed exclosures near and in trees, this association is not surprising. Cache locations

were associated with canonical axis 1 (66%), suggesting that rodents preferentially

cached seeds in areas with logs, herbaceous cover, and denser canopy cover. Random

locations were negatively associated with canonical axis 1 (-70%) and therefore

associated with woody cover. ANOVA corroborated the difference between cache sites

and random locations for logs (F=8.172, p=0.006) and canopy density (F=4.466,

p=0.039) but not for herbaceous cover (F= 2.8 p=0.1).

Discussion

Seeds were frequently removed and deposited intact at distances up to 42.6 m

from the exclosures. Carvajal and Adler (2008) found similar removal distances on Barro

Colorado Island in central Panama. Although most seeds were simply left by the removal

agents on top of the leaf litter, some were pushed into the leaf litter, while others

frequently settled into the soil after prolonged heavy rains during the rainy season. The

most likely removal agents were spiny rats and squirrels. In fact, I suggest that *P.*

semispinosus and *S. granatensis* are the primary removal agents not only of *A. butyracea*

and *A. standleyanum* seeds but indeed of other large-seeded species in the second-growth

forests along Pipeline Road. This suggestion is contrary to recent generalizations that

agoutis (*Dasyprocta punctata*) are the primary dispersers of large-seeded palms in

Panamanian forests (Jansen *et al*. 2012). Supporting my suggestion are recent

experiments in which agoutis were allowed the opportunity to remove seeds, but removal

rates did not increase above rates when they were excluded (Lambert *et al*. 2014). I

further suggest that the relative importance of dispersal agents is likely to vary spatially

and temporally, depending upon season, climatic perturbations, forest structure, rodent

abundance, and local behavioral adaptations of such rodents. Therefore, it is unwise to

assume that a particular species will always be the most important dispersal agent in a

given region.

Of the two rodents in this study, *P. semispinosus* was likely the more important

removal agent of seeds from exclosures over the study period, based on our abundance

data. *Proechimys semispinosus* was approximately 7-fold more abundant than *S.

granatensis*. Other species were either too small to remove the seeds or apparently were

transient in the study area. For instance, *H. gymnurus* was unlikely to be a permanent

resident within the study area because it is restricted to cool, moist microhabitats along

streams and steep ravines (Tomblin & Adler 1998; Adler *et al*. 1998). The two

individuals that were caught within the study area were likely moving between streams.

Although *D. oleifera* seeds were the only large seeds available during the dry

season, they were removed much less frequently than those of *A. butyracea* or *A.

standleyanum*. This surprising result may be due to two reasons that are not mutually

exclusive. First, all *D. oleifera* seeds collected for the study already had the fruit

removed. I was unable to locate any seeds in which the fleshy mesocarp had not already

been eaten by an animal. Mesocarp absence could decrease their ability to be detected, particularly by olfaction. Second, the study plots did not have any *D. oleifera* trees located within them. Rodents within the plots may not have actively searched for *D. oleifera* because of this absence, instead focusing on other food sources within the plots.

Differences in the distances moved by *A. standleyanum* and *A. butyracea* are puzzling because *A. butyracea* produces a larger and heavier seed, yet its seeds were moved farther than those of *A. standleyanum*. One possible reason for this difference could be abundance of both plants. *Astrocaryum standleyanum* were much more abundant within the study sites than *A. butyracea*. It may not have been beneficial to rodents to move *A. standleyanum* seeds very far because it would not decrease the density of seeds because they were likely to encounter a parent tree with a high density of seeds underneath. With *A. butyracea,* rodents were less likely to encounter a parent tree, so moving seeds away from the source would decrease seed density. An alternative explanation is that *A. butyracea* is a preferred food source, so it is to the benefit of the rodent to better conceal them by spacing deposition sites.

Seeds were more frequently dropped or cached by *P. semispinosus* and *S. granatensis* in locations of greater herbaceous cover and denser canopy cover and near logs greater than 10 cm in diameter (Figure 2). Unsurprisingly, those variables describe microhabitats with which both species are associated. *Sciurus granatensis* is more abundant in humid forests characterized by high canopy of deciduous and evergreen trees, with a secondary sub-story primarily dominated by palms and variable understory (Glanz 1984). *Proechimys semispinosus* is associated with younger, more disturbed forest

characterized by tree-fall gaps, lower canopies, and higher densities of smaller trees, logs, and lianas (Lambert & Adler 2000). Such microhabitats are common along Pipeline Road.

In contrast to previous studies, I found no association between seed cache location and tree-fall gaps or lianas (Kilgore *et al.* 2010; Carvajal & Adler 2008). The lack of association with gaps may be due to differences in forest structure between study sites; there are fewer and smaller gaps in the younger forest along Pipeline Road (personal observation) than on older forest on Barro Colorado, where Carvajal and Adler (2008) performed their study.

Deposited seeds were never buried during this study, nor did it appear that any attempt was made to conceal the seed under leaf litter or other objects (only one seed was found under leaf litter). This lack of concealment is in stark contrast to what has been observed on Barro Colorado Island (ca. 14 km from my study site), where *P. semispinosus* and *S. granatensis* actively bury seeds in the soil or in leaf litter (Forget *et al.* 1994; Carvajal & Adler, 2008). It is unlikely that the attached bobbin would affect the rodents' caching behavior. Mean distance moved did not differ from Carvajal and Adler (2008), who used a short piece of thread attached to seeds to locate them, suggesting that the bobbin method did not hinder the rodents in seed movement. Even if the bobbin did make it more difficult for the rodents to bury seeds in the soil, it is unlikely to have had any effect on their ability to cover the seeds with leaf litter. One potential cause for the lack of burial could be related to perceived predation risk. Rodents will alter their foraging habits and habitat use when perceived predation risk is high (Brown 1988;

Brown *et al.* 1988; Longland & Price 1991; Pierce *et al.* 1992). Forests along Pipeline

Road have a more intact predator community than does Barro Colorado Island (Terborgh

1992; Wright *et al.* 1994; Wright *et al.* 1999). Because predators are more diverse and

abundant along Pipeline Road, rodents may have to adjust their caching behavior to

minimize predation risk. Burying seeds therefore may expose rodents to greater predation

risks, and such risks are minimized by only placing seeds on or into the leaf litter.

Furthermore, rodents removed the exocarp and mesocarp from many of the seeds that

they transported, thereby rendering them less attractive to other potential seed predators.

My study supports the observation that smaller rodents are not strictly predators

of seeds (Hoch & Adler 1997; Adler & Kestell 1998; Forget 1991a; Forget & Milleron

1991), unlike previous suggestions that such rodents are unimportant in dispersal of large

seeds (reviewed in Vander Wall *et al.* 2005). In fact, under favorable conditions, the

relationship may be strongly mutualistic. During the study period, only one seed of *D.*

oleifera was preyed upon. All *A. butyracea* and *A. standleyanum* seeds had only the

fleshy mesocarp removed, and the seed itself was never damaged during removal. While

I was unable to successfully follow long-term seed fate, seeds could be followed for

approximately one month after removal; re-caching was rare, and consumption of such

seeds by mammals did not occur. Low initial seed consumption was also observed during

a similar study by Kilgore *et al.* (2010), in contrast to what was found on Barro Colorado

Island with *P. semispinosus, S. granatensis*, and the larger agoutis (Carvajal & Adler

2008; Jansen *et al. 2012)*. In Carvajal and Adler (2008), the majority of seeds harvested

by *P. semispinosus and S. granatensis* were eaten and never cached. In Jansen *et*

al.(2012), initial seed predation was low, but within one week, 57% of all monitored caches were re-cached, with 13% of the seeds being consumed after the primary caching event. Eventually, 99% of the seeds cached in the Jansen *et al.* (2012) study were recovered, but 14% survived for one year. With such low predation rates in our study and low removal rates by agouties in the same area (Lambert *et al.* 2014), it is possible that the smaller rodents such as *P. semispinosus* and *S. granatensis* play a more important role than agoutis in the forest of my study area. Short-term cache removal appears to be low along Pipeline Road, and its effects on seed fate are unknown. Future studies are needed to follow the fate of the seeds deposited by *P. semispinosus* and *S. granatensis* to determine long-term recovery rates and seedling survival in such deposits.

Chapter III

General Conclusions

My study has shown that two small rodents in central Panama likely have a mutualistic relationship with large-seeded trees. Although my experimental design precluded determining long-term seed fates, the habits of these rodents are congruent with what would be predicted by the hypotheses of seed dispersal from chapter I. Specifically, I believe that this mutualism has been formed and maintained through a combination of all three hypotheses.

Both species of palms and *D. oleifera* exhibit strong negative Janzen-Connell effects (Cintra 1997; Silvius 2005). These plants all produce large, heavy seeds that rarely fall outside of the tree crown and often accumulate in high densities. The piles of seeds underneath parent plants act as magnets that attract predators, which cause high mortality rates. By dispersing these seeds, *P. semispinosus* and *S. granatensis* are likely decreasing Janzen-Connell effects. In this study, seeds were rarely moved more than 10 m in a single event, but with the addition of subsequent events, a small proportion of seeds had been moved tens of meters away from the source. Away from a parent plant, these seeds are less prominent to predators and may have increased survival.

Evidence for directed dispersal was the main goal of this study, and there is strong evidence for it. Rodents preferentially placed seeds in locations that had large logs and thicker herbaceous cover and not located near large trees. While there was no association with tree gaps (measurement of canopy density) in this study, other studies have found

these rodents to be associated with such gaps (Glanz 1984; Tomblin & Adler 1998; Lambert & Adler 2000; Adler 2000). Gaps with which *P. semispinosus* were associated also exhibited high log densities. Although there were no tree falls within the study plots during the study period, small rodent preference for gaps may cause directed dispersal to gaps when present because they share similar characteristics with preferred seed deposition sites found in this study. This apparent preference is potentially important because many of these trees are light-dependent (Araus & Hogan 1994; Hogan 1988) and have little chance of survival under thick canopy. Tree gaps potentially offer the perfect suite of protection (high liana, log densities, high herbaceous cover, and ample sunlight) for these large-seeded trees to establish.

Evidence for the colonization hypothesis was not the goal of this study, and little inference can be made on its effectiveness in forming or maintaining the mutualism. However, both species of rodents rarely larder-hoarded seeds during the study and were effective at scattering seeds away from the source. If colonization is an ecologically-important issue for a plant species, it would be beneficial for it to maximize mutualisms with animals that scatter-hoard seeds rather than larder-hoard them. This habit increases the probability of a single seed reaching a location that is suitable or may become suitable in the future.

Finally, these plants have evolved seed and fruit characteristics that are congruent with maintaining mutualistic relationships. All three species of trees studied have large seeds that are well protected by a stony endocarp. The seeds are surrounded by fleshy mesocarps that are bright in coloration, odoriferous, and nutritious. These characteristics

are essential for attracting mammals, and by producing nutritious fruits, the plants may be able to decrease the amount of predation on the seed. If the plant species were trying to escape predation (i.e., no dispersal advantages) it would be expected that the fruits would be reduced or lost completely so that they are not attractive to mammals.

Variable	Abbreviation	Description
1. Tree Distance	tdist	Mean distance of the nearest trees ($\geq$ 10cm dbh) in all 4 cardinal directions from site
2. Tree Diameter	tdiam	Mean diameter of the nearest trees ($\geq$ 10cm dbh) in all 4 cardinal directions from site
3. Number of Lianas	tvine, tvinec	Mean number of lianas in contact with 4 trees described above. Also the number of vines from the center and within a 5m radius from center.
4. Herbaceous cover	herb	Number of herbaceous plants intersected by a 5m rope strung out in all 4 cardinal directions from site
5. Woody Cover	wood	Number of woody plants intersected by a 5m rope strung out in all 4 cardinal directions from site
6. Duff	duff	The mean depth of leaf litter taken at two points (2.5m & 5m) along a 5m rope strung out in all 4 cardinal directions from site
7. Number of Logs	log	Number of logs ($\geq$ 10cm diameter) intersected by a 5m rope strung out in all 4 cardinal directions from site
8. Canopy Density	dens	Mean density of the forest canopy measured at 5m out from site in all 4 cardinal directions and at the center site
9. Number of Saplings	sap	Mean number of saplings found within 2.5m of either side of a 5m rope strung out in all 4 cardinal directions from the center and within a 5m radius from the center.

Table 1: Description of the data collected for microhabitat analysis.

Variable	Significant Source Effects	χ^2	P
All rodents	None	N/A	N/A
Proechimys semispinosus	Plot & Time	32.73 & 6.75	<0.0001 & 0.009
Sciurus granatensis	None	N/A	N/A
Fruit	Plot	41.17	<0.0001
Seeds removed	Plot	10.80	0.055*
	All Rodents, Rats, Squirrels	28.94, 23.75, & 25.60	0.0003, 0.0047, & <0.0001

Table 2: Summary of significant source effects of each variable using log linear analysis.

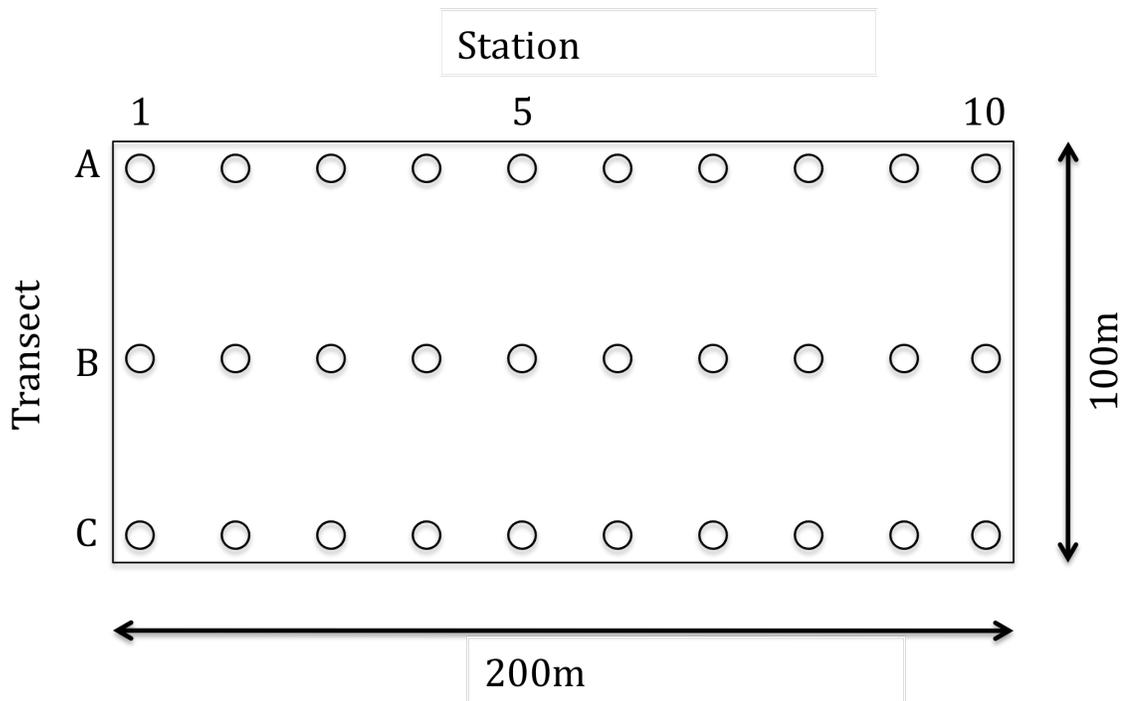* denotes an effect that was not significant but marginal.

Figure 1:
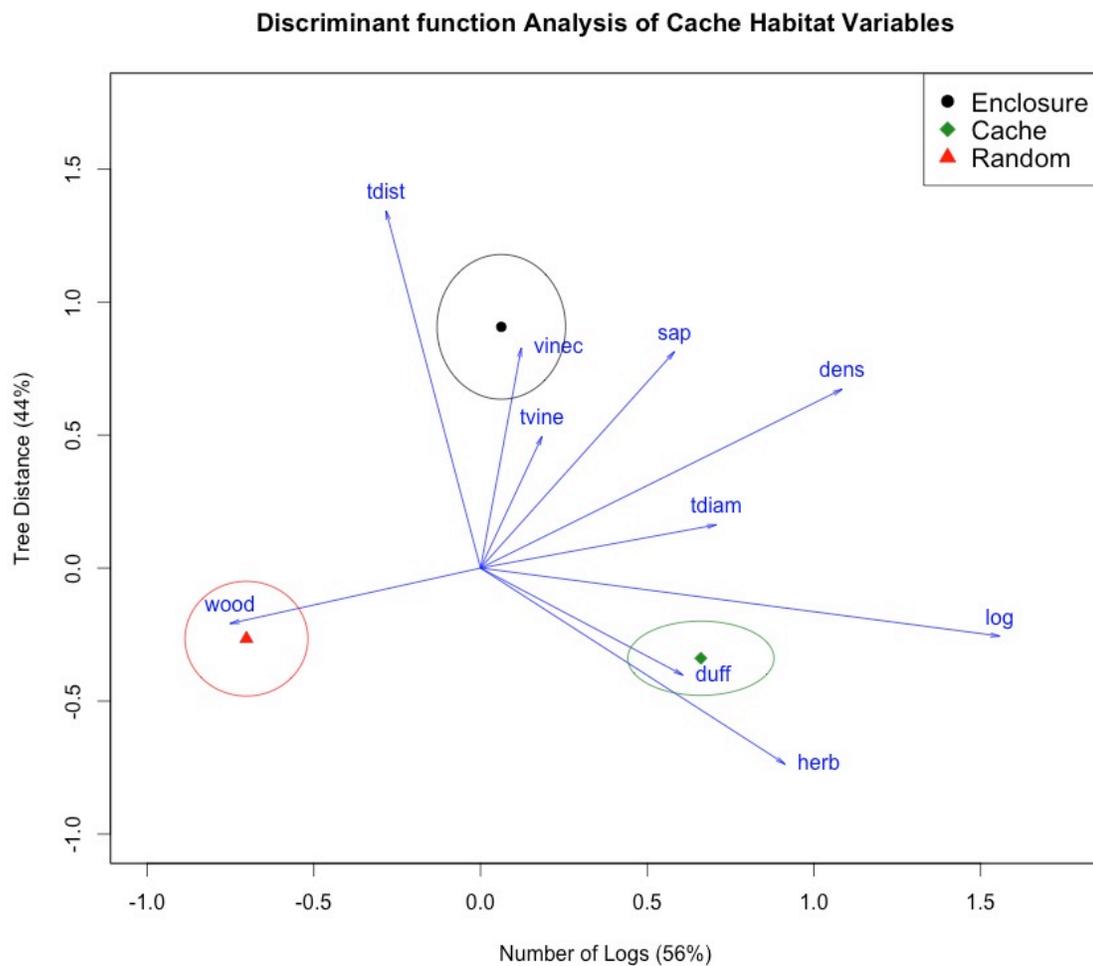
Schematic diagram of plot design.

Figure 2:

Plot of the discriminant function analysis of microhabitat data. Ellipses represent standard errors. Variables correspond to microhabitat measurements in Table 2. Wilk's Lambda = 0.569, P = 0.0145

References

Adler, G.H. 1995. Fruit and Seed Exploitation by Central American Spiny Rats,

    Proechimys semispinosus. Studies on Neotropical Fauna & Environment 30(4):

    237 – 244.

Adler, G.H. 1998. Impacts of resource abundance on populations of a tropical forest

    rodent. Ecology 79(1): 242 – 254.

Adler, G.H. 2000. Tropical tree diversity, forest structure and the demography of a

    fruigivorous rodent, the spiny rat (*Proechimys semispinosus*). *Journal of Zoology*

    250(01): 57 – 74.

Adler, G.H. and D.W. Kestell. 1998. Fates of neotropical tree seeds influenced by spiny

    rats (*Proechimys semispinosus*). Biotropica 30(4): 677 – 681.

Adler, G. H., D. C. Tomblin, and T. D. Lambert. 1998. Ecology of two species of

    Echimyid rodents (*Hoplomys gymnurus* and *Proechimys semispinosus*) in central

    Panama. *Journal of tropical ecology* 14(5): 711 – 717.

Araus, J.L., and K. P. Hogan. 1994. Leaf structure and patterns of photoinhibition in two neotropical palms in clearings and forest understory during the dry season. *American Journal of Botonay* 81: 726 - 738

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22(1): 37 – 47.

Brown, J.S., B.P. Kotler, R.J. Smith, and W.O. Wirtz II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia* 76(3): 408 – 415.

Carvajal, A. and G. H. Adler. 2008. Seed dispersal and predation by *Proechimys semispinosus* and *Sciurus granatensis* in gaps and understory in central Panama. *Journal of Tropical Ecology* 24: 485-492.

Cintra, R. 1997. A test of Janzen-Connell model with two common tree species in Amazonian forest. *Journal of Tropical Ecology* 13: 641 – 658.

Clark, D.B. and D.A. Clark. 1984. Spacing dynamics of a tropical rain forest tree; evaluation of the Janzen-Connel model. American Naturalist 124: 769 – 788.

Connell J. H. 1971. On the role of natural enemies in preventing competitive exclusion
in some marine animals and in rain forest trees. In P.J. den Boer and G. Gradwell
(Eds.) *Dynamics of numbers in populations*, pgs 298 – 312. Center for Agricultural
Publication and Documentation, Washington.

Flagel, D., G. H. Adler, and T. D. Lambert. 2009. Influence of seed height on removal
rates by rodents in central Panama. *Mammalia* 73(1): 76 – 77.

Forget, P.-M. 1991a. Scatterhoarding of *Astrocaryum paramaca* by *Proechimys* in French
Guiana: Comparison with *Myoprocta exilis*. *Tropical Ecology* 32: 155 – 167.

Forget, P.-M. 1991b. Comparative recruitment patterns of two non-pioneer canopy tree
species in French Guiana. *Oecologia* 85: 434 – 439.

Forget, P.-M. and T. Milleron. 1991. Evidence for secondary seed dispersal by rodents in
Panama. *Oecologia* 87: 596 – 599.

Forget, P.-M., E. Munoz, and E.G. Leigh Jr. 1994. Predation by rodents and bruchid
beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panama. *Biotropica*
26(4): 420 – 426.

Glanz, W. E., R. W. Thorington, J. Giacalone-Madden and L.R. Henry. 1982. Season Food Use and Demographic Trends in *Sciurus granatensis*. In E.G.L., A.S.R., and D.M.W. (Eds.). *The Ecology of Tropical Forest*, pgs 239 – 251. Smithsonian Institution Press, Washington.

Glanz, W. E. 1984. Food and habitat use by two sympatric *Sciurus* species in central Panama. *Journal of Mammalogy* 65(2): 342 – 347.

Harms, K.E. and J.W. Dalling. 2000. A bruchid beetle and a viable seedling from a single disapore of *Attelea butyracea. Journal of Tropical Ecology* 16: 319 – 325.

Heaney, L.R. and R.W. Thorington Jr. 1978. Ecology of Neotropical Squirrels, *Sciurus granatensis*, in the Panama Canal Zone. Journal of Mammalogy 59(4): 846 – 851.

Hoch, G.A. and G.H. Adler. 1997. Removal of Black Palm (*Astrocaryum standleyanum*) by spiny rats (*Proechimys semispinosus*). *Journal of Tropical Ecology* 13(1): 51 – 58.

Hogan, K.P. 1988. Photosynthesis in two neotropical palm species. *Functional Ecology* 2: 371 – 377.

Howe, H.F. 1986. Seed dispersal by fruit-eating birds and mammals. In Seed Dispersal
D.R. Murray (Ed). pp. 123–189. Sydney, NSW: Academic Press.

Howe, H.F. and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of
Ecology and Systematics 13: 201-228.

Hume, P.E. 1994. Post-Dispersal Seed Predation in Grassland: It's Magnitude and
Sources of Variation. *Journal of Ecology* 82(3): 645-652.

Jansen, P. A., B.T. Hirsch, W. Emsens, V. Zamora-Gutierrez, M. Wikelski, and R. Kays.
2012. Thieving rodents as substitute dispersers of megafaunal seeds. *PNAS*
109(31): 12610 – 12615.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests.
American Naturalist 104: 501 – 528.

Karr, J.R. 1990. The avifauna of Barro Colorado and the Pipeline Road. In A.H (Ed),
Four Neotropical Forests. Yale University Press, New Haven, CT, USA.

Kilgore, A., T. D. Lambert, and G. H. Adler. 2010. Lianas influence fruit and seed use by
rodents in a tropical forest. *Tropical Ecology* 51(2): 265 – 271.

Lambert, T. D., and G. H. Adler. 2000. Microhabitat use by a tropical forest rodent, *Proechimys semispinosus*, in central Panama. *Journal of Mammalogy* 81(1): 70 – 76.

Lambert, T.D., J.R. Malcolm, and B.L. Zimmerman. 2005. Variation in small mammal species richness by trap height and trap type in southeastern Amazonia. Journal of Mammalogy 86: 982-990.

Lambert, T. D., K. L. Sumpter, J. W. Dittel, S. Dupre, K. Casanova, A. Winker, and G.H. Adler. 2014. Roads as barriers to seed dispersal by small mammals in a neotropical forest. *Tropical Ecology* 55(2): 263 – 269.

Laurance, W.F., D. Perez-Salicrup, P. DeLamonica, P.M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T.E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82(1): 105 – 116.

Longland, W.S. and M.V. Price. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology* 72(6): 2261 – 2273.

Pierce, B.M. and W.S. Longland. 1992. Rattlesnake predation on desert rodents: microhabitat and species-specific effects on risk.

Silvius, K. M. 2005. Frugivore-mediated interactions among bruchid beetles and palm fruits at Barro Colorado Island, Panama: implications for seed fate. In P.-M. Forget (ed) *Seed Fate: Predation, Dispersal, and Seedling Establishment*, pgs 45 – 54. CABI Publishing, Wallingford.

Terborgh, J. 1970. Seed and fruit dispersal – Commentary. In K.S. Bawa, K. Bawa, and M. Hadley (Eds.). *Reproductive ecology of tropical forest plants*. United Nations Educational Scientific and Cultural Organization, Paris.

Terborgh, J. 1992. Maintenance of diviersity in tropical forests. *Biotropica* 24(2b): 283 – 292.

Terborgh, J., E. Losos, M. P. Riley, and M Balanos Riley. 1993. Predation by vertebrates and invertebrates on the seeds of five Canopy tree species of an Amazonian forest. *Vegetatio* 107/108: 375 - 386.

Tomblin, D.C. and G. H. Adler. 1998. Differences in habitat use between two morphologically similar tropical forest rodents. *Journal of Mammalogy* 79(3): 953 – 9661.

Vandermeer, J.H. 1979. Hoarding Behavior of Captive *Heteromys demarestianus* (Rodentia) on the Fruits of *Welfia georgii*. *Tropical Ecology* 20: 17-26.

Vander Wall, S.B., Kuhn, K.M., and Beck, M.J. 2005. Seed survival, seed predation, and secondary dispersal. *Ecology* 86: 801 – 806.

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

Wright, S.J. 1983. The dispersion of eggs by a bruchid beetle along *Scheelea* palm seeds and the effect of distance to the parent palm. *Ecology* 64: 1016 – 1021.

Wright, S.J., M.E. Gompper, and B. DeLeon. 1994. Are large predators keystone species in Neotropical forests? The evidence from Barro Colorado Island. *Oikos* 71: 279 – 294.

Wright, S. J., C. Carrasco, O. Calderon, and S. Patton. 1999. The El Nino southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80: 1632 – 16.