

Seed dispersal by rodents in a lowland forest in central Panama

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Abstract: We studied the removal of seeds of three species of large-seeded tree (*Astrocaryum standleyanum*, *Attalea butyracea* and *Dipteryx oleifera*) from three different heights within six study plots in a lowland forest in central Panama. Fresh fruits with intact seeds fitted with industrial sewing bobbins were placed within semi-permeable exclosures. Removed seeds were tracked to deposition sites, and seed fate was determined. Removals were likely perpetrated by two small rodents, the strictly terrestrial *Proechimys semispinosus* and the scansorial *Sciurus granatensis*, because they were the most abundant small rodents in the study site during the study period and were of sufficient size to remove large seeds. Rodent abundance and fruit availability were estimated by conducting censuses. Nine microhabitat variables were measured at each deposition site to determine if these two rodents were preferentially depositing seeds in sites with certain characteristics or were randomly depositing seeds. During the study, rodents handled 98 seeds, 85 of which were not predated upon and could potentially germinate. Removal rates were not influenced by rodent abundance or fruit availability. Seeds were most frequently moved < 3 m and deposited with the fruit eaten and the seed intact. However, some seeds did experience relatively long-distance dispersal (> 10 m). Rodents preferentially deposited seeds in locations with large logs (> 10 cm diameter), dense herbaceous cover, and an intact canopy. The number of large logs was different from random locations. Despite not being able to determine long-term fate (greater than c. 1 y), we show that these small rodents are not primarily seed predators and may in fact be important mutualists by dispersing seeds relatively long distances to favourable germination sites.

Key Words: *Astrocaryum standleyanum*, *Attalea butyracea*, Panama, *Proechimys semispinosus*, red-tailed squirrel, *Sciurus granatensis*, seed dispersal, seed predation, spiny rat

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 1990). Small rodents, owing to their diversity, ubiquity and abundance in most tropical forests, typically remove vast numbers of seeds in such forests. Small rodents generally have been considered to be seed predators rather than dispersal agents (Hulme 1994, Terborgh *et al.* 1993, Vandermeer 1979; but see Vander Wall *et al.* 2005). However, there is an increasing amount of work showing that tropical rodents previously thought to be solely seed predators are in fact also important seed dispersers (Adler & Kestell 1998, Carvajal & Adler 2008, Forget 1991a, Hoch & Adler 1997, Jansen *et al.*

2012, Kilgore *et al.* 2010, Lambert *et al.* 2014). In central Panama, two presumably important rodent seed dispersers are the terrestrial Central American spiny rat (*Proechimys semispinosus*) and the scansorial red-tailed squirrel (*Sciurus granatensis*). Both species scatter-hoard seeds (Adler & Kestell 1998, Carvajal & Adler 2008, Heaney & Thorington 1978, Hoch & Adler 1997, Kilgore *et al.* 2010) and their activities could have major impacts on tropical plant distributions (Carvajal & Adler 2008).

Previous studies have examined seed removal by these two rodents. Hoch & Adler (1997) found a positive association between spiny rat abundance and removal rate of *Astrocaryum standleyanum* seeds and also documented scatter-hoarding and seed burial by *P. semispinosus*. Carvajal & Adler (2008) studied seed-removal differences between *P. semispinosus* and *S. granatensis*. Not only did both species remove seeds, but they also scatter-hoarded them by placing them under leaf litter and burying them in the soil. Rodents that hide seeds

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in this manner may increase plant fitness by decreasing the probability of desiccation and predation, thereby facilitating germination and survival (Forget 1991a, b; Forget & Milleron 1991, Forget *et al.* 1994). Additionally, Flagel *et al.* (2009) examined the influence of seed placement height (ground, subcanopy and canopy) on the removal rates of two species of palm (*A. standleyanum* and *Attalea butyracea*) in central Panama. Seed removal occurred not only after the seed had fallen but also while still in the tree, thereby necessitating the study of all phases of a seed's life.

Unfortunately, the extent to which these two common and widely distributed rodents influence long-term seed fates is poorly known. Such information is sorely needed, given the ubiquity, abundance and importance of such rodents in influencing seed fates and ultimately forest regeneration. Accordingly, our aim was to incorporate three aspects of seed removal (seed placement height, microhabitat of deposition site and seed fate) by *P. semispinosus* and *S. granatensis* into one study to develop a better understanding of the role that small mammals in general might play in tropical forest regeneration. We hypothesize that if ripe fruits are present at different heights (canopy, subcanopy and ground), then removal rates will differ among heights because rodent abundances vary with height. We also hypothesize that if *P. semispinosus* and *S. granatensis* are scatter-hoarding large-seeded plants, then seeds will not be cached in random locations across the forest but rather at locations that correlate with the preferred habitat of these rodents (Adler 2000, Beck *et al.* 2004, Lambert & Adler 2000, Tomblin & Adler 1998) and in sites that are favourable for germination.

MATERIALS AND METHODS

Study site

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 from 30 to 200 m asl (Karr 1990). Mean annual rainfall is approximately 2612 mm, based upon 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 was once a paved road but now receives only desultory maintenance and

is consequently severely degraded. The road runs south-east to north-west through the northern section of the park and allows ready access to a portion of the forest.

Along Pipeline Road, six study plots, each measuring 100 m wide by 200 m long, were randomly positioned, three on each side of the road (east and west). Each plot contained three transects (designated A, B and C) marked at 0, 50 and 100 m, and each transect contained 10 sampling stations spaced at 20-m intervals.

Study species

Three common species of tree in Soberanía National Park, 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 palm produce large fruits (c. 4 × 3 cm for *A. standleyanum* and 6 × 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 × 2.5 cm and contain single seeds. Unlike most fruiting plants in central Panama, this tree fruits just after the onset 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).

We focused the study on *P. semispinosus* and *S. granatensis* based on their abundance within the study site and many lowland tropical forests (Kilgore *et al.* 2010). Both species have a generalized diet that includes both the fruits and seeds of the majority of tropical trees, typically preferring large-seeded species (Adler 1995, Glanz 1984) and are potentially important in seed removal (Carvajal & Adler 2008, Flagel *et al.* 2009, Kilgore *et al.* 2010). 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 and sometimes scatter-hoards seeds on the ground. It also caches seeds in trees (Carvajal & Adler 2008, Heaney & Thorington 1978). Larder-hoarding, whereby 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 ultimately consumed, buried too deep to germinate if not immediately consumed or stored in trees where rooting cannot occur.

Rodent sampling

Spiny rat abundance was estimated by live trapping on the six study plots. One Tomahawk live-trap ($40.5 \times 12.6 \times 13$ cm, Tomahawk, WI, USA) was placed at each station within a plot, 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, KY, 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 were difficult to sample by live trapping (Carvajal & Adler 2008). To estimate relative abundance, sight surveys were performed by walking along each transect within a study plot once per week during each field season. Surveys were complemented by stopping at stations two, five and eight on the B transect of each plot and sitting quietly for 20 min at each station.

Fruit availability

Fruit availability was estimated by walking along the transects within each plot. 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 season (before, during, and after the seed removal period) and twice in the dry season (before and after the removal period).

Seed removal and tracking

We used Tomahawk live-traps wired open as semipermeable enclosures to admit rodents smaller than c. 800 g. Five ripe fruits (with the seed) from a single species were placed within the enclosures for 20 d. Fruits of *A. standleyanum*, followed by those of *A. butyracea*, were used during the rainy season for a total of 40 d, and fruits of *D. oleifera* were used during the dry season for 20 d. 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 seven 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 unravelling and to secure the bobbin to the wire. The bobbins contained approximately 200 m of thread, which was much greater than the predicted distance that seeds would travel (Carvajal & Adler 2008). The loose end of the bobbin thread was tied to the seed enclosure such that the thread could be followed to final seed placement. Nine seed enclosures were placed within each study plot along the B transect at station two, midway between stations five and six, and at station eight. Three seed enclosures were placed at varying heights at each station. Enclosures were placed on the ground (0 m), in the subcanopy (up to 5 m above ground), and in the canopy (>5 m above ground). Enclosures at the subcanopy level were fixed to lianas or tree branches with bungee cords, while enclosures in the canopy were raised by rope until they rested securely against a large tree branch or liana so that rodents travelling through the canopy could readily enter the enclosure (Flagel *et al.* 2009, Kilgore *et al.* 2010, Lambert *et al.* 2005). Seed enclosures were checked daily, and fruits that were removed, eaten in the enclosure, rotten, or infested with mould were replaced with fresh fruit. We tracked each removed seed by following the thread to its final deposition site, and all such sites were marked with a pin flag.

Seed removal distances and fates and microhabitat characteristics

For seeds that could be located, the linear distance moved and direction from the enclosure were recorded, and a seed fate was determined. Fates included fruit and seed intact, fruit eaten and seed intact, and seed destroyed (either consumed at the deposition site or larder-hoarded). 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 seed that was located, the thread was detached from the enclosure and reattached to a nearby plant to allow the tracking of any potential future movements. Seed locations were marked with pin flags, and seed fates were monitored daily. All seeds that were moved again were assigned to the same fate categories as the seeds from the enclosures. If the seed was moved again, the event was considered to represent secondary removal. If multiple seeds were cached in a single location, only one microhabitat data point was measured to avoid problems associated with dependence. Pin flags were maintained in place between field seasons to facilitate finding scatter-hoarded seeds and establishing long-term fates. If such seeds were found, then their fate was recorded as previously described.

Nine different microhabitat variables from five different sections (for a total of 45 measurements) were

Table 1. Description of the data collected for microhabitat analysis along Pipeline Road, Panama. The first column is the name of the variable, followed by the abbreviation used in this paper and a brief description.

Variable	Abbreviation	Description
Tree distance	tdist	Mean distance of the nearest trees (≥ 10 cm dbh) in all four cardinal directions from cache
Tree diameter	tdiam	Mean diameter of the nearest trees (≥ 100 cm dbh) in all four cardinal directions from cache
Number of lianas	tvine, tvinec	Mean number of lianas in contact with four trees described above. Also the number of lianas within 5 m radius of cache
Herbaceous cover	herb	Number of herbaceous plants intersected by a 5-m rope strung out in all four cardinal directions from cache
Woody cover	wood	Number of woody plants intersected by a 5-m rope strung out in all four cardinal directions from cache
Duff	duff	The mean depth of leaf litter taken at two points (2.5 m and 5 m along a rope strung out in all four cardinal directions from cache
Number of logs	log	Number of logs (≥ 10 cm diameter) intersected by a 5-m rope strung out in all four cardinal direction from cache
Canopy density	dens	Mean density of the forest canopy measured at 5-m out from the cache in all four cardinal directions and at cache
Number of saplings	sap	Mean number of saplings found within 2.5 m of either side of a 5-m rope strung out in all four cardinal directions from the cache

measured at each enclosure, each seed-deposition site, and a randomly selected location (Table 1). Thus, the deposition site of each removed seed was paired with both the enclosure from which it originated and a random location. Random locations were determined by randomly selecting a compass direction and moving the same distance to which a seed was moved from the enclosure. Canopy density was estimated using a densiometer, which was a small (approximately 10 cm diameter) convex mirror with a 1×1 -cm grid etched into it. 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 centre. For secondary-removal events in which the seed remained intact, microhabitat data at the seed's new location were recorded and combined with data from the primary-removal events.

Data analysis

Spiny rat abundance was estimated as the number of different individuals captured on a plot over the course of a 10-d sampling session (Carvajal & Adler 2008). Statistical estimators of abundance were not applicable because of the long time interval between subsequent samplings and the consequent low numbers of recaptures. Squirrel abundance similarly was estimated as the total number of squirrels sighted on a plot during a census. Rodent abundance (*P. semispinosus* and *S. granatensis* separately and both species combined) and fruit availability, all recorded as counts, were analysed by constructing full log-linear models that included plot and year as main effects and the plot \times year interaction. We searched for associations between the numbers of seeds removed from a plot and abundances of *P. semispinosus*, *S. granatensis*,

all rodents combined, and total fruit availability and per capita fruit availability for *P. semispinosus*, *S. granatensis*, and all rodents combined using Pearson product-moment correlation analysis. Per capita fruit availability was calculated by dividing fruit availability by the number of rodents in each of the three categories. We included estimates only from the two rainy-season samples ($N = 12$ observations) and computed seven such correlations.

Mean distances that seeds were moved were compared between palm species and between years using *t*-tests. Removal distances were used to estimate kernel densities (K_D), thereby allowing us to predict the relative probability that a seed would be moved to a given distance, based on the area under the curve (Weiblen & Thompson 1995). We used a Gaussian smoothing kernel to create the curve using the density function in Program R based on Clark *et al.* (1999). Due to the small number of removed *D. oleifera* seeds, this species was excluded from all analysis of removal distance.

Removed seeds were placed into a combination of three fate (fruit and seed intact, fruit eaten and seed intact and seed destroyed) and two distance (≤ 3 m and > 3 m) categories. The three fate and two distance categories resulted in six cells, and the distribution of seeds among fate-distance cells was compared using log-linear analysis.

Microhabitat data were analysed using backward elimination three-group discriminant function analysis (DFA) to search for patterns in the distribution of seed deposition sites according to microhabitat structure. Enclosure locations, seed deposition sites and random locations composed the three groups. Variables that were retained in the model were then analysed 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-enclosure

station. All microhabitat data of seed-deposition sites were omitted if the seed was moved from the seed-exclosure station less than 3 m to reduce the problem of dependence.

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

RESULTS

Rodent abundance

We accumulated a total of 7200 trap nights during rodent live-trapping. *Proechimys semispinosus* was the most frequently captured rodent, with a total of 142 individuals captured over the four sampling seasons. The only other species of rodent captured during the study period were two individual *Hoplomys gymnurus* (armoured rat) and one individual *S. granatensis*. We observed 28 *S. granatensis* during 40 h 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 ($\chi^2 = 5.70$, $P = 0.336$; $\chi^2 = 4.14$, $P = 0.529$, respectively) or years ($\chi^2 = 7.61$, $P = 0.179$; $\chi^2 = 1.88$, $P = 0.391$) and there were no interactions ($\chi^2 = 5.90$, $P = 0.823$; $\chi^2 = 1.56$, $P = 0.212$). However, abundance of *P. semispinosus* did vary among plots ($\chi^2 = 32.7$, $P < 0.0001$). Plot 6 had the most *P. semispinosus*, while plot 2 had the fewest. Abundance of *P. semispinosus* also differed between years ($\chi^2 = 6.75$, $P = 0.009$), but there was no plot \times year interaction ($\chi^2 = 3.08$, $P = 0.0793$).

Fruit availability

Fruit availability was much greater during the rainy seasons ($\bar{x} = 25.2$ fruiting plants per plot) than during the dry seasons ($\bar{x} = 5.6$ fruiting plants per plot). Availability differed among plots ($\chi^2 = 41.2$, $P < 0.001$) but not between years ($\chi^2 = 1.06$, $P = 0.302$). Plot five produced the most fruit, while plot one produced the least. However, there was an interaction between plot and year ($\chi^2 = 14.5$, $P = 0.0129$).

Seed removal

In 27 000 fruit days (where one fruit day is equivalent to a single fruit available for 1 d), 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 subcanopy and four from the canopy. All subcanopy and canopy seeds were assumed to have been removed by *S. granatensis* because *P. semispinosus* is strictly terrestrial. Five seeds removed from the ground were carried into the canopy and therefore were most likely removed by *S. granatensis*. Seeds removed from and deposited on the ground most likely were handled by *P. semispinosus* based on its abundance and body size. Correlation analysis revealed no associations between the numbers of seeds removed from a plot and the seven rodent abundance and fruit availability variables ($r < 0.56$, $P > 0.06$ in all correlations). There was no plot effect on removal ($\chi^2 = 10.8$, $P = 0.055$). Most removed seeds that we successfully tracked were placed on top of the leaf litter and were never buried in the soil. We 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 97 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. There was a difference in distance moved between species ($t = 3.45$, $P = 0.0013$) but not between years ($t = 1.35$, $P = 0.1840$). *Attalea 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.

Kernel density estimates showed that most seeds of both species were moved to distances within the extent of a parental tree crown (Figure 1). However, a small proportion of seeds were indeed moved well beyond that distance.

The distribution of seeds among fate and distance categories differed ($\chi^2 = 67.7$, $P < 0.0001$). Most seeds were moved a short distance (< 3 m) and were deposited with the fruit eaten but the seed left intact. The next greatest portion of seeds was moved a longer distance (> 3 m) and deposited with the fruit eaten but the seed intact. We were unable to determine longer-term fates of most 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 study (*c.* 1.5 y), but none of those seeds

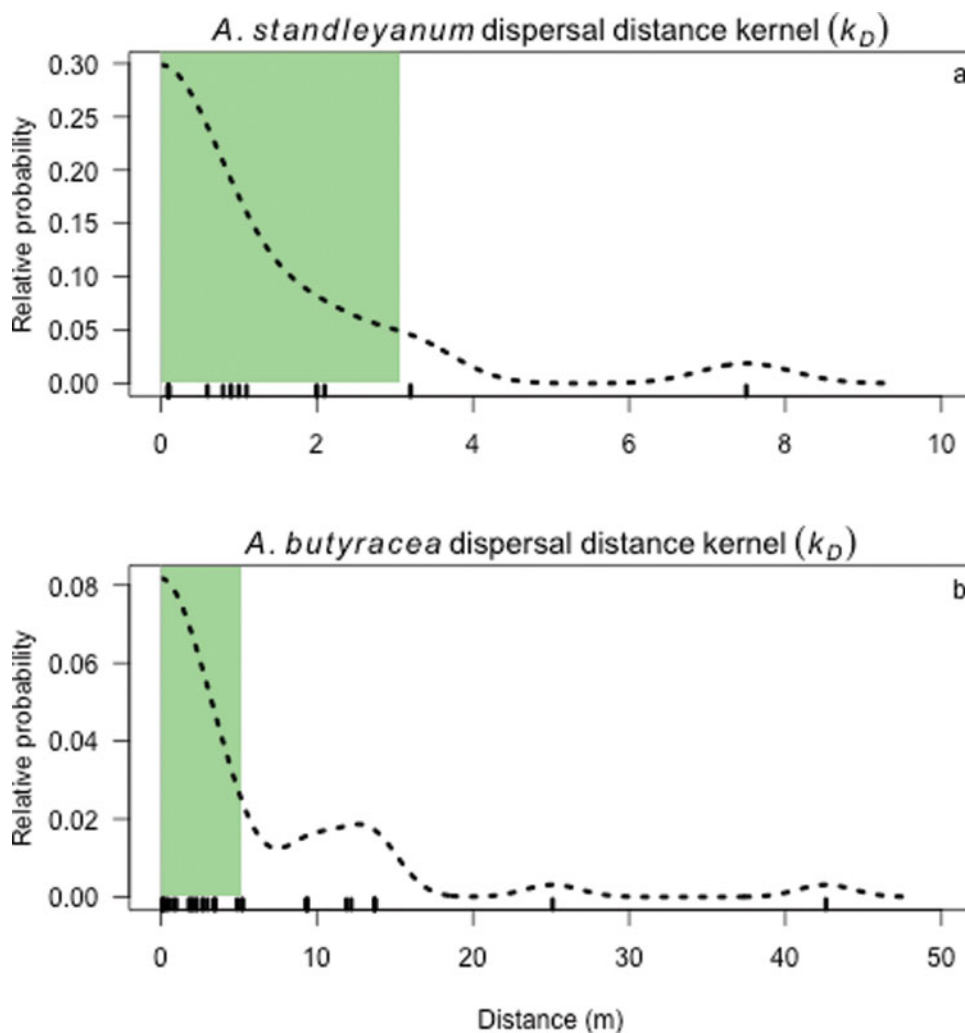


Figure 1. Plot of the kernel density estimates (K_D) of *Astrocarylum standleyanum* (a) and *Attalea butyracea* (b) from Pipeline Road, Panama. The dotted line represents the relative probability that a seed will be deposited at a given distance. The shaded box represents the radius of the crown of the tree. Hashes at the bottom of the graph represent the actual distances moved by a seed during this study.

germinated. Of the *A. standleyanum* and *A. butyracea* seeds that were removed during the first rainy season (50 seeds), nine were still present in the subsequent dry season, and of those nine seeds, five were present at the end of the study. Of the 12 *D. oleifera* seeds that were removed, four seeds were present at the end of the study. However, the hole in the seeds exposed them to small predators and fungal growth, and such seeds did not germinate and were likely unpalatable to rodents before re-caching or consumption could occur.

Of the 97 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. DFA, with 28 observations in each group, yielded a first canonical axis that explained 56% of the variance, while the second

canonical axis explained 44% (Figure 2). The number of logs >10 cm, canopy density and herbaceous cover were most closely associated with the first axis, while distance to the nearest tree and tree diameter were most closely associated with the second axis. The DFA model had significant discriminatory power (Wilk's Lambda = 0.569, $P = 0.0145$). Group centroids (exclosure, deposition and random groups) therefore strongly differed from one another, and the standard error of the means did not overlap (Figure 2). Seed exclosure locations were associated with tree distance (second axis). Because we intentionally placed exclosures near and in trees, this association was not surprising. Seeds were deposited in sites with more logs and greater herbaceous and canopy cover (first axis) relative to random locations. Random locations were negatively associated with woody cover (axis one). ANOVA corroborated the difference between cache sites and random locations for logs ($F = 8.17$,

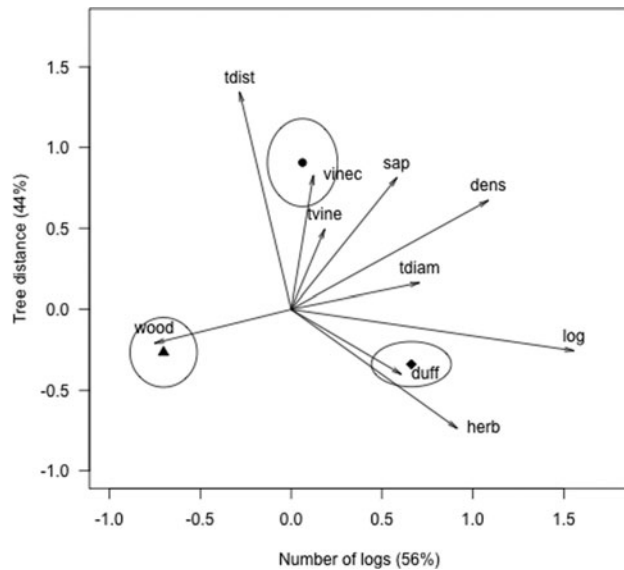


Figure 2. Plot of the discriminant function analysis of microhabitat data from Pipeline Road, Panama. A circle represents the enclosure, a diamond represents a deposited seed location, and a triangle represents a random location. Ellipses represent standard errors. Variables correspond to microhabitat measurements in Table 1. Wilk's Lambda = 0.569, $P = 0.0145$.

$P = 0.006$) and canopy density ($F = 4.47$, $P = 0.039$) but not for herbaceous cover ($F = 2.8$, $P = 0.1$).

DISCUSSION

Seed removal rates were lower relative to other studies in central Panama (Asquith *et al.* 1997, Hoch & Adler 1997), although those studies were conducted on very small islands where rodent abundances were greater. Despite the lower removal rates, seeds in this study were frequently deposited intact at distances up to 42.6 m from the enclosures. Removal rates and distances were similar to those found by Carvajal & Adler (2008) 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 litter, while others rapidly settled into the soil after prolonged heavy rains during the rainy season. The most likely removal agents were spiny rat and red-tailed squirrel. In fact, we suggest that *P. semispinosus* and *S. granatensis* are the primary removal agents not only of *A. butyracea*, *A. standleyanum* and *D. oleifera* seeds but indeed of many other large-seeded species in the second-growth forests along Pipeline Road. This suggestion is contrary to a recent generalization that the agouti (*Dasyprocta punctata*) is the primary disperser of large-seeded palms in Panamanian forests (Jansen *et al.* 2012). Supporting our suggestion are recent experiments in the same forest along Pipeline Road 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). Although we frequently encountered agoutis, we suggest that they were considerably less abundant, largely because of hunting by humans, than on Barro Colorado Island, where Jansen *et al.* (2012) conducted their study. We further suggest that the relative importance of dispersal agents is likely to vary spatially and temporally, depending upon season, climatic perturbations (e.g. ENSO events), forest structure, rodent abundance and local behavioural 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 forest.

Of the two rodents in this study, *P. semispinosus* was likely the more important removal agent of seeds from enclosures over the study period, based on our abundance data. Other species were either too small to remove the seeds or apparently were transient or rare in the study area. For instance, *H. gymmurus* was unlikely to be a permanent resident within the study area because it is largely restricted to cool, moist microhabitats along streams and steep ravines (Adler *et al.* 1998, Tomblin & Adler 1998). The two individuals that were caught within the study area were likely moving between streams. Other small rodents present in the study area (Tomblin & Adler 1998), such as *Heteromys desmarestianus* (forest spiny pocket rat) were too small to remove the study seeds. Seed removal was not associated with rodent abundance, fruit abundance, or per capita fruit availability. This seemingly surprising result may be due to the small sample of only six plots sampled in two seasons, providing only a snapshot of a continuous phenomenon.

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 result may be due to two reasons that are not mutually exclusive. First, we were unable to locate any *D. oleifera* seeds in which the fleshy mesocarp had not already been consumed 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, although these trees occur elsewhere along Pipeline Road. 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 the abundance of both plants. *Astrocaryum standleyanum* was much more abundant within the study sites than was *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, as 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 and therefore the likelihood of cache discovery by a different individual. An alternative explanation is that fruits and seeds of *A. butyracea* are preferred (Lambert *et al.* 2014), so it is to the benefit of the rodent to better conceal them by spacing deposition sites. Lastly, there is evidence that *S. granatensis* moves seeds farther than does *P. semispinosus* (Carvajal & Adler 2008); if so, then observed differences in dispersal distances of the seeds of these two species of palm in the forest along Pipeline Road could be explained by the preference of *S. granatensis* for *A. butyracea* seeds and its subsequent greater removal distances.

The kernel density estimates (Figure 1) show that most palm seeds are not moved beyond the extent of the crown of parental plants. This short movement is detrimental to the palms because both species exhibit strong negative Janzen–Connell effects (Cintra 1997, Silvius 2005). However, a small proportion of seeds are moved beyond the crown, thereby increasing the probability that those seeds can avoid Janzen–Connell effects. Thus, seeds that are moved outward from beneath the crown and therefore away from the parent plant should have a greater probability of surviving (Clark & Clark 1984). While the number of such seeds in our study is small, when one considers the thousands of seeds produced over the lifetime of an individual plant, we suggest that the benefits that *P. semispinosus* and *S. granatensis* have on seed survival are substantial.

Seeds were not moved to random locations but were instead more frequently deposited in locations with greater herbaceous cover, denser canopy cover and near logs greater than 10 cm in diameter (Figure 2). Such non-random depositions of seeds could represent directed seed dispersal. Unsurprisingly, those variables describe microhabitats with which both rodent species are associated. *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); other members of the genus show similar habitat associations (Beck *et al.* 2004). *Sciurus granatensis* is more abundant in forests characterized by a higher canopy of deciduous and evergreen trees, with a dense understorey primarily dominated by palms (Glanz 1984). Such microhabitats are common along Pipeline Road. The proximity of seed caches near logs also was observed by Kiltie (1981). Such placement is of interest because rodents may use landmarks as markers to remember cache placement, which in turn may aid seed predators in detecting seeds and seedlings (Beck & Terborgh 2002, Kiltie 1981).

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 (c. 14 km from study site) and smaller nearby islands, where *P. semispinosus* and *S. granatensis* actively bury seeds in the soil or in leaf litter (Adler & Kestell 1998, Carvajal & Adler 2008, Forget *et al.* 1994, Hoch & Adler 1997). It is unlikely that the attached bobbin would affect the rodents' caching behaviour. Mean distance moved did not differ from Carvajal & 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 render 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 Barro Colorado Island (Terborgh 1992, Wright *et al.* 1994, 1999) and smaller islands (Adler 1996). Because predators are more diverse and abundant along Pipeline Road, rodents may have to adjust their caching behaviour to minimize predation risk. Burying seeds therefore may expose rodents to greater predation risk, and such risk is minimized by only placing seeds on or into the leaf litter. Furthermore, rodents removed the exocarp and mesocarp from all of the seeds that they transported, thereby rendering them less attractive to other potential seed predators.

Our study supports the observation that smaller rodents such as spiny rats and squirrels are not strictly predators of seeds (Adler & Kestell 1998, Forget 1991a, Forget & Milleron 1991, Hoch & Adler 1997), unlike previous suggestions that such rodents are unimportant in dispersal of large seeds (reviewed in Vander Wall *et al.* 2005). In fact, under favourable conditions, the relationship may be strongly mutualistic. During the study period, only one seed of *D. oleifera* was preyed upon. All transported *A. standleyanum* and *A. butyracea* seeds had only the fleshy mesocarp removed, and the seed itself was never damaged during removal. While we were unable to document germination, seeds could be followed for up to 1.5 y after initial 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 results from Barro Colorado Island with *P. semispinosus*, *S. granatensis* and the larger *D. punctata* (Carvajal & Adler 2008, Jansen *et al.* 2012). Short-term cache removal appears to be generally low along Pipeline Road, and

its effects on seed fate are unknown. Future studies are needed to better follow the fates of seeds deposited by *P. semispinosus* and *S. granatensis* to determine long-term recovery rates and seedling survival and to better understand caching differences among populations of *P. semispinosus*.

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