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Seed dispersal and predation by *Proechimys semispinosus* and *Sciurus granatensis* in gaps and understorey in central Panama

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Abstract: Seed dispersal and predation by spiny rats (*Proechimys semispinosus*) and red-tailed squirrels (*Sciurus granatensis*) were studied in five forest gaps and adjacent forest understorey on Barro Colorado Island, Panama, during June and July 2003 and January 2004. Live trapping on grids was used to estimate the abundances of rats in both habitats and was conducted during 10 nights at the beginning of each field season. We captured 70 individual spiny rats (53 in forest gaps and 17 in understorey). To address the removal and dispersal of seeds, semi-permeable wire-mesh exclosures were set at randomly selected stations within the trapping grids. These exclosures allowed the entry of spiny rats, squirrels, and other small rodents but excluded larger granivorous mammals. Seeds were marked with pieces of string that were dusted with fluorescent powder and tracked at night with an ultraviolet light. A total of 304 seeds was removed (159 in forest gaps and 145 in understorey). Spiny rats removed more seeds from gaps, and squirrels removed more seeds from understorey. Both species dispersed more seeds during the rainy season than during the dry season. Squirrels dispersed seeds farther than did spiny rats. Due to their foraging behaviour and association with gaps, spiny rats may disperse seeds from forest understorey into gaps.

Key Words: Barro Colorado Island, Central American spiny rat, forest gaps, red-tailed squirrel, seed fate, seed removal

INTRODUCTION

Tropical forests are the most complex ecosystems on earth because of their extraordinary diversity of species and the vast array of interactions among those species and between them and the environment (De Steven 1988). These interspecific interactions are woven together to form an intricate fabric of complexity that is still very poorly understood. Understanding how tropical forests regenerate following disturbance has become a central issue in tropical and conservation biology, and it is increasingly evident that interspecific interactions are important in determining the trajectories of forest regeneration. For example, the probability of tree seedling establishment and the subsequent distribution of adult trees are thought to depend largely on the interrelationship between organisms that serve as seed dispersers and those that function as mortality agents (Augspurger 1983, 1984; Augspurger & Kelly 1984, Connell 1971, Janzen 1970).

Rodents are especially important in this regard because many species are abundant and function as both seed dispersers by moving seeds from one place to another (Adler & Kestell 1998, Forget & Milleron 1991, Jansen *et al.* 2004, Smythe 1989) and as mortality agents by consuming seeds (Adler & Kestell 1998, Forget *et al.* 1994, Hoch & Adler 1997, Jansen *et al.* 2004). Such opposing roles exhibited by rodents have been demonstrated experimentally to influence seed and seedling survival (Asquith & Mejía-Chang 2005, Asquith *et al.* 1997, De Steven & Putz 1984, Smythe 1989, Terborgh & Wright 1994). In general, studies on predation and dispersal of seeds of tropical trees by mammals have focused on larger species of rodents (Forget 1990, 1996; Larson & Howe 1987, Smythe 1986, 1989), while the role of smaller rodents as dispersal agents has been largely overlooked because of the assumption that such rodents are mainly seed predators (Vander Wall *et al.* 2005). Small rodents can attain greater relative abundances and biomass than

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larger species of rodents, and their foraging habits may have a tremendous impact on seed survival and seedling establishment (Brewer & Rejmánek 1999, Brewer *et al.* 1997).

Despite a fairly substantial body of experimental studies on seed predation and dispersal in tropical forests, the natural history of the agents of predation and dispersal often is documented poorly. Information gleaned from experimental studies may be augmented by concurrently acquiring natural history data on rodents, including their use of different habitats. Although seed removal rates have been compared between gaps or disturbed forest and adjacent forest understorey (Beck & Terborgh 2002, De Steven & Putz 1984, Schupp *et al.* 1989), fates of removed seeds were not examined.

This study addresses the habitat distribution of a common forest rodent, the Central American spiny rat (*Proechimys semispinosus*), and its role as a seed predator and disperser. Spiny rats consume seeds from a wide variety of forest plants (Adler 1995), disperse seeds without destroying them (Adler & Kestell 1998, Hoch & Adler 1997), and are statistically associated with tree-fall gaps and young forest (Adler 2000, Lambert & Adler 2000, Tomblin & Adler 1998). Disturbed areas of the forest are exposed to increased direct sunlight and exhibit increased plant recruitment. Most species of tropical tree require those conditions to reach maturity (Denslow 1987, Schupp *et al.* 1989). If spiny rats are indeed more common in such gaps and disperse seeds from forest understorey into gaps, then their influence on forest regeneration will be enhanced. Such activities may increase seedling establishment and growth and promote forest regeneration (Lambert & Adler 2000). Other species of small rodent (e.g. the red-tailed squirrel, *Sciurus granatensis*) are more abundant in intact forest (Reid 1997). Accordingly, we also include data on seed predation and dispersal by *S. granatensis*, a species with a well-known natural history (Glanz 1984, Glanz *et al.* 1996, Heaney & Thorington 1978).

We hypothesized that (1) abundances of *P. semispinosus* would be greater in tree-fall gaps than in forest understorey, in accordance with previous studies (Lambert & Adler 2000), (2) rates of seed removal by spiny rats would be greater in gaps, (3) rates of seed removal by red-tailed squirrels would be greater in forest understorey, and (4) both species would function as both seed predators and dispersal agents.

METHODS

Study site

The study was conducted on Barro Colorado Island (BCI), Panama. Barro Colorado Island is a 1500-ha island, the largest of over 200 hilltops that were isolated as islands during the final stages of the creation of the Panama Canal when the Chagres River was dammed in 1914 to form Gatun Lake (Adler & Seamon 1991, Leigh 1999). The island is covered with both old-growth and second-growth tropical moist forest. Despite the reduced area, the mammal community on the island is typical of larger tracts of forest, with two exceptions: (1) populations of once-present large predators, the puma (*Puma concolor*) and the jaguar (*Panthera onca*), are generally absent from BCI but still persist on the adjacent mainland and occasionally visit the island, and (2) most species of herbivore and frugivore are still present, with some of them maintaining higher densities than on the mainland (Wright *et al.* 1999, Wright & Duber 2001), although white-lipped peccaries (*Dicotyles pecari*) have been extirpated from the area.

Central Panama experiences pronounced seasonality with respect to precipitation. A severe 4-mo dry season from January to April is followed by 8 rainy months, during which approximately 90% of the precipitation occurs (Rand & Rand 1996, Windsor 1990). There is also great seasonal variability in the abundance of fruit available to the potential dispersers in the forest, and at the end of the rainy season and beginning of the dry season, there is a shortage of fruit in the forest. There are two peaks of fruiting. The first and broader one occurs between March and June, and the second one in September and October (De Steven *et al.* 1987, Foster 1996).

Rodent species

Proechimys semispinosus is widely distributed from Honduras southward to north-western South America to the west of the western Andes. It is typically one of the most abundant rodents in lowland tropical forests, ranging from highly disturbed second-growth to old-growth forests (Adler 2000, Eisenberg 1989, Emmons & Feer 1997). *Proechimys semispinosus* is strictly terrestrial and mostly nocturnal. This rodent consumes seeds from a wide variety of forest plants (Adler 1995) and also scatterhoards seeds without destroying them (Adler & Kestell 1998, Hoch & Adler 1997).

The distribution of *S. granatensis* in Central America coincides with that of *P. semispinosus*. In South America, however, *S. granatensis* is more widely distributed, extending to the valleys between the Andean ranges and eastward to northern Venezuela (Eisenberg 1989, Emmons & Feer 1997). This diurnal rodent feeds on a variety of fruits and seeds, but those of four tree species (*Attalea butyracea*, *Astrocaryum standleyanum*, *Dipteryx oleifera*, and *Gustavia superba*) compose most of its diet (Glanz *et al.* 1996). The red-tailed squirrel is largely arboreal, but it frequently forages on the ground. It also caches seeds in the ground and in trees (Heaney & Thorington 1978, Reid 1997).

Live trapping

Spiny rats were sampled by live-trapping on paired plots in five different locations on BCI, with one such plot located within a tree-fall gap of approximately 0.2–0.3 ha and the second plot located within forest understorey 50 m from the plot in the gap. Each plot consisted of a 5 × 5 grid of sampling stations, with an inter-station distance of 10 m. Plots within gaps were centred on the gap. Each sampling station was occupied by a single Tomahawk live-trap (40.5 × 12.6 × 13 cm, Tomahawk, Wisconsin, USA) placed on the ground. The traps were baited with cut ripe bananas, set for 10 consecutive nights, and checked each morning in June 2003 and January 2004. All captured rats were ear-tagged with a small, serially numbered metal tag (National Band and Tag Co., Newport, Kentucky, USA) for individual identification, weighed, and immediately released at the station of capture. Red-tailed squirrels could not be effectively sampled by live trapping but were frequently sighted within the sampling sites.

Seed removal

To assess removal and dispersal of seeds, we established experiments at each pair of sampling grids after rodent sampling was completed so that capturing the rodents would not interfere with the experiments. Fruits of the species *Attalea butyracea* (Arecaceae) (June and July 2003) and *Dipteryx oleifera* (Papilionaceae) (January 2004) were used in the experiments. These trees are large-seeded species common on BCI, and both mesocarp (pulp) and seeds are consumed by *P. semispinosus* (Adler 1995) and *S. granatensis* (Glanz *et al.* 1996, Heaney & Thorington 1978).

Attalea butyracea palms produce abundant fruit from May through October, with a fruiting peak usually during June and July (De Steven *et al.* 1987, Adler & Lambert 2008). The fruits are oblong in shape and usually contain one large seed (6 cm × 3 cm), protected by a hard endocarp. The physiology and architecture of *A. butyracea* suggest that this species is well suited to exploit higher-light environments such as tree-fall gaps (Araus & Hogan 1994, Hogan 1988).

Dipteryx oleifera is one of the very few large-seeded (5–6 cm × 2–3 cm), animal-dispersed trees that fruits early in the dry season when food resources are scarce (Croat 1978) and experiences high seed predation by terrestrial and arboreal mammals (Forget 1993). The drupes of *D. oleifera* are elliptical and have sweet, green pulp covered by a thin membranous exocarp (Croat 1978, Forget 1993).

We randomly selected five stations within each grid to place piles of 10 seeds on the forest floor and covered the seeds with a wire mesh exclosure (30.5 × 30.0 × 15.0 cm) with an opening (8.0 × 6.0 cm) that allowed entry of *P. semispinosus* and *S. granatensis* (and other small rodents, which were too small to remove the large fruits and seeds included in the study) but excluded larger frugivorous mammals such as agouti (*Dasyprocta punctata*), paca (*Agouti paca*), and collared peccary (*Tayassu tajacu*). The exclosures were staked firmly to the ground.

The fruits used in the experiments were collected beneath parent trees and taken to the laboratory to be marked. Whenever possible, fresh fruits were used. However, towards the end of the fruiting season, refrigerated fruits were used. Whole fruits rather than seeds were used because the presence of the pulp may affect the feeding behaviour of rodents (Guimarães *et al.* 2005). To mark the fruits, a single thread approximately 40 cm in length was attached to each fruit using a small metal screw inserted into the endocarp, and the threads were dusted with pink fluorescent powder that glows brightly under ultraviolet light.

Every night or every other night, we counted the number of intact fruits present in each of the exclosures and tracked the removed fruits with an ultraviolet light (Adler & Kestell 1998, Hoch & Adler 1997). The seeds were tracked easily because a trail of dust remained on the forest floor, even after heavy rains, as the seeds were carried away. The removal agent also was readily determined because spiny rats produced trails of evenly spaced tracks solely on the forest floor, while squirrels produced unevenly spaced tracks that frequently ascended trees. The fates of the removed seeds were assigned to previously established categories: (1) eaten *in situ*, (2) removed and eaten elsewhere, (3) discarded on top of the leaf litter, (4) larderhoarded (carried into subterranean burrows), and (5) scatterhoarded (hidden under the leaf litter or buried in the ground). The location of each scatterhoarded seed was marked and checked periodically until the end of the field season. We also measured the linear distance of each such seed from its station of removal to its burial site.

Data analysis

Data analysis focused on three aspects of the study: (1) abundance of spiny rats on grids located within forest understorey and tree-fall gaps, (2) seed removal by *P. semispinosus* and *S. granatensis* and the fates of those seeds, and (3) distance of dispersal by both species of rodent. All analyses were conducted using SAS version 9.1.2 (SAS Institute, Cary, NC, USA).

Chi-square analysis was used to search for differences in the distribution of rats between forest types (forest understorey or forest gap). The analysis was conducted separately for the two sampling seasons.

Linear analysis for categorical data was used to model seed fate. This technique is appropriate for cases in which independence may be violated (Lindsey 1995) when the same individual rats and squirrels may have repeatedly removed seeds. We included fate as the dependent variable and rodent species (squirrel or rat) and forest type (understorey or gap) nested within season (rainy or dry) as the independent variables, weighted by counts according to seed fate. For this analysis, seed fates were combined into two categories, scatterhoarded (i.e. effectively dispersed) and destroyed (i.e. eaten, larderhoarded, or removed but not buried). Seeds that were left on top of the leaf litter, carried into trees (by *S. granatensis*) or larderhoarded were grouped in the new category 'destroyed' because they were inefficiently dispersed and would not germinate successfully or would be vulnerable to predation (Adler & Kestell 1998). Seeds that were scatterhoarded were considered to have been dispersed successfully. Only those seeds for which removal agent and fate could be determined were included in the analysis.

We used analysis of variance (ANOVA) to search for differences in the mean dispersal distance of scatterhoarded seeds between rodent species and seasons. Distances were $\log_{10}$-transformed. We constructed a saturated model that included both main effects (species and season) and the interaction term.

RESULTS

Live trapping

We captured 70 individual *P. semispinosus* over the two sampling periods (Table 1). No individuals were captured on more than one sampling grid. We also captured four Talamancan rice rats (*Oryzomys talamancae*) in June 2003. Spiny rats were more abundant in tree-fall gaps than in forest understorey in both the rainy ($\chi^2 = 8.76$, df = 1, P = 0.0031) and dry seasons ($\chi^2 = 9.76$, df = 1, P = 0.0018). Abundance of squirrels could not be assessed accurately, but we sighted squirrels much more frequently in forest surrounding the gaps than within the gaps.

Table 1. Numbers of *Proechimys semispinosus* captured according to season and habitat (gap and understorey).

Season	Gap	Understorey	Total
June–July 2003	25	8	33
January 2004	28	9	37
Total	53	17	70

Table 2. Numbers of removed seeds of *Attalea butyracea* and *Dipteryx oleifera* sorted by fate and forest type. P.s. = *Proechimys semispinosus*; S.g. = *Sciurus granatensis*; Un. = Unknown.

	Gap			Understorey			
Fate	P.s.	S.g.	Un.	P.s.	S.g.	Un.	Total
Scatterhoarded	9	4	0	10	12	0	35
Larderhoarded	7	0	0	1	0	0	8
Eaten	27	17	1	8	22	1	76
Moved	23	15	1	12	24	0	75
Unknown	1	8	46	2	10	43	110
	67	44	48	33	68	44	
Total		159			145		304

Seed removal

A total of 304 of the 1500 seeds placed in the exclosures was removed during the study (Table 2). In 191 cases, both the fate and removal agent could be determined. Disturbance of the exclosures (despite the fact that they were staked to the ground) during the seed-removal experiments resulted in some missing seeds of which the fate and/or removal agent could not be determined. We could not determine the removal agent in 89 cases. In 21 cases, although the removal agent was identified, the seed could not be found, and the fate was recorded as 'unknown'. In only three cases, the seed was found and the fate determined, but the removal agent could not be identified. Although all seeds could not be assigned to a fate category or a removal agent, our sample sizes were sufficient to obtain robust statistical significance.

Most of the seeds removed by *P. semispinosus* and *S. granatensis* were eaten or deposited on top of the leaf litter (equal numbers of seeds in each category, summing to 77.4%). A smaller percentage of the seeds was scatterhoarded (18.3%), and only 4.2% of the seeds were larderhoarded.

There were statistical differences in the patterns of seed removal and scatterhoarding between spiny rats and squirrels. Rats removed more seeds from gaps, squirrels removed more seeds from forest understorey, and more seeds were scatterhoarded during the rainy season than during the dry season ($\chi^2 = 12.5$, df = 4, P = 0.0142). Red-tailed squirrels scatterhoarded seeds at greater distances (N = 14, mean ± SD = 9.71 ± 4.36 m) than spiny rats (N = 19, mean ± SD = 6.08 ± 7.06 m) (F = 6.53, df = 1, P = 0.0157), but there was no effect of season on dispersal distance (F = 2.72, df = 3, P = 0.0629).

Spiny rats removed a total of 100 seeds during the study, but only 19 seeds were scatterhoarded. All caches by *P. semispinosus* were terrestrial. Of the scatterhoarded seeds, nine were actually buried in the soil, while the remainder were hidden just under the leaf litter (eight seeds) or under very thick vine tangles (two seeds). In most cases, the seeds were cached after the fleshy mesocarp had been removed.

Red-tailed squirrels cached seeds both on the ground and in trees. Seeds in arboreal caches were not considered scatterhoarded because they had little probability of survival and germination, and most of them were retrieved and eaten within the following 24–48 h. Those temporary caches were usually in tree cavities and branch forks. Despite their arboreal habits, the number of seeds scatterhoarded in the ground by *S. granatensis* (16 seeds, 14.2%) did not differ greatly from the number of seeds scatterhoarded by *P. semispinosus*. However, the characteristics of the caches were different. Red-tailed squirrels generally buried seeds at the base of a tree, against buttresses, or pushed between a liana and the soil.

DISCUSSION

In our study area, spiny rats were clearly more abundant in tree-fall gaps than in understorey forest. Of the 70 individuals captured, 75.7% were captured in gaps. Previous studies on habitat use by *P. semispinosus* conducted on BCI and the adjacent mainland reported similar results. Spiny rats were associated with young forest and tree-fall gaps (Lambert & Adler 2000, Tomblin & Adler 1998, Adler unpubl. data). However, those studies used transects for sampling rodents and quantifying habitat structure, and paired sampling data were lacking. On trapping grids on smaller islands in Lake Gatun, Panama, spiny rats were most abundant on islands with forest cover of intermediate age (Adler 2000). Other species of spiny rat also use gaps extensively (Beck *et al.* 2004, Emmons 1982).

The paired-plot experimental design used in this study allowed for a better comparison of the relative abundances of rats in gaps and forest understorey. Using this method, we demonstrated more conclusively that spiny rats indeed were associated with gaps. Although we did not rigorously assess the relative abundance of *S. granatensis* in the two microhabitats studied (gaps and understorey) because they are difficult to trap, it was apparent from the seed removal data and personal observations that *S. granatensis* foraged more frequently in forest than in gaps.

Overall seed predation in this study was intermediate (38.7%) relative to other studies. Observed predation by small mammals may be as low as 7% (Forget 1991a) or may exceed 90% (De Steven & Putz 1984). It is difficult to compare studies because predation may vary greatly among sites, plant species, dispersers, years and seasons (Holl & Lulow 1997). In fact, the percentage of seeds that were eaten during the dry season, when food was scarce, was greater than during the rainy season. This pattern has been reported previously (Brewer & Rejmánek 1999).

Scatterhoarding behaviour by small rodents frequently has been overlooked because such rodents generally have been considered seed predators rather than seed dispersers (Vander Wall *et al.* 2005). Among small rodents, spiny rats and red-tailed squirrels are important seed removal agents, but their caching behaviour has not been studied rigorously. Although previously considered mainly seed predators and seed larderhoarders, rodents in the genus *Proechimys* have been the subject of studies on seed dispersal since their scatterhoarding behaviour was described first by Forget (1991a). It was reported that *P. semispinosus* cached seeds under the leaf litter (Hoch & Adler 1997), but in this study we found that they also buried seeds in the soil. This behaviour is of importance to the trees because, although not all tree species require seed burial to successfully germinate, burying seeds may prevent desiccation, facilitate germination and rooting, and reduce the probability of post-dispersal predation (Forget 1991a, b; Forget *et al.* 1994, Forget & Milleron 1991). In this study, spiny rats scatterhoarded only 19 seeds. Although seemingly a small number, 19% of all seeds removed by spiny rats were scatterhoarded. Thus, the total number of seeds scatterhoarded throughout the forest by these abundant rodents may be substantial.

Few accounts of caching by *S. granatensis* are available in the recent literature. However, earlier descriptive studies provide a point of comparison. The caching behaviour and the characteristics of the arboreal and terrestrial caches observed in this study correspond with those of Heaney & Thorington (1978). The number of seeds scatterhoarded by red-tailed squirrels is slightly fewer than that of spiny rats, but nonetheless, the two species combined scatterhoarded 18.3% of the seeds they removed. Even agoutis and other larger frugivores considered important dispersal agents of large-seeded species can destroy a large percentage of seeds, but it is the small percentage that is scatterhoarded and the even smaller percentage that survive post-dispersal mortality that will result in new recruits (Brewer *et al.* 1997). Although this study did not follow the seeds to germination or seedling establishment, *P. semispinosus* and *S. granatensis* may be considered reliable dispersers of large-seeded species such as those used in this study. Caching behaviour also was affected by seasonality. More seeds were scatterhoarded during the rainy season, when food in the forest was abundant, and it is unlikely that this difference was due to seed species.

Thus, both species of rodent included in this study occur syntopically, use similar food resources, and are very similar in body mass (adult body weight *c.* 300–500 g, Emmons & Feer 1997). However, the two species exploit overlapping food resources at different temporal and spatial scales. *Proechimys semispinosus* is a nocturnal, terrestrial species associated with gaps, whereas *S. granatensis* is a diurnal, terrestrial and arboreal species that typically forages in more intact areas of the forest. Knowledge of the natural histories of the two species of tree may further enhance our understanding of the roles the two species of rodent play in dispersing seeds.

Dipteryx oleifera is an important food resource for frugivores and granivores, including *S. granatensis* and *P. semispinosus*, during the dry season when other fruits are scarce (Croat 1978). It experiences frequent seed predation and also high post-germination mortality (Clark & Clark 1984, 1987; De Steven & Putz 1984). Density-dependent mortality may be related to pathogens and granivores, and dispersal away from sites with high densities of seeds may improve seed survival. There is controversy over whether *D. oleifera* is a shade-tolerant or gap species. It is clear that the seeds can germinate and seedlings can establish successfully in shaded areas, but increased exposure to light is an important factor in promoting growth of smaller saplings (<10 mm dbh), and both diameter and height are greater in early successional sites than in mature forests (Clark & Clark 1987). Thus, the scatterhoarding behaviour of spiny rats and their association with gaps may confer an advantage to the seeds they disperse. The level of exposure to light will change as the gap matures and succession proceeds. However, dispersal of *D. oleifera* seeds to open habitats may increase the probability of survival if increased growth occurs and the saplings can reach a diameter and height at which mortality is greatly reduced.

Attalea butyracea produces large numbers of fruit at the beginning of the rainy season when fruit in the forest is abundant (Adler & Lambert 2008). Despite the abundance of food available to frugivores, seeds of *A. butyracea* experience frequent predation. The concentration of fruit around the parent tree attracts granivores that can destroy most of the seeds (Bradford & Smith 1977). *Attalea butyracea* fruits are an important food item in the diet of *P. semispinosus* and *S. granatensis*, and their role as secondary dispersers of this palm may increase the survival of the seeds. Carrying the fruits away from the parent tree to a site with lower concentration of fruit and lower seed predation could increase the probability of germination and seedling establishment. *Attalea butyracea* also exhibits structural and physiological characteristics that suggest that this species may be better adapted to gaps and high-sunlight environments (Araus & Hogan 1994, Hogan 1988). Thus, the foraging behaviour of *P. semispinosus*, particularly its association with gaps, may confer an additional advantage to the seeds of *D. oleifera* and *A. butyracea* by moving them to environments with increased sunlight, which may result in faster growth.

We did not specifically address directed dispersal by either species of rodent. However, results of the present study, when coupled with previous studies on the ecology of spiny rats, suggest that these rodents not only remove seeds from gaps but could potentially import seeds into gaps, where their caching behaviour would enhance the probability of successful germination. Future studies should address directed dispersal, and understanding such phenomena requires detailed knowledge of the natural histories of both the plants and their potential seed dispersers and mortality agents.

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