

Mammal Abundances and Seed Traits Control the Seed Dispersal and Predation Roles of Terrestrial Mammals in a Costa Rican Forest

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ABSTRACT

In Neotropical forests, mammals act as seed dispersers and predators. To prevent seed predation and promote dispersal, seeds exhibit physical or chemical defenses. Collared peccaries (*Pecari tajacu*) cannot eat some hard seeds, but can digest chemically defended seeds. Central American agoutis (*Dasyprocta punctata*) gnaw through hard-walled seeds, but cannot consume chemically defended seeds. The objectives of this study were to determine relative peccary and agouti abundances within a lowland forest in Costa Rica and to assess how these two mammals affect the survival of large seeds that have no defenses (*Iriartea deltoidea*, *Socratea exorrhiza*), physical defenses (*Astrocaryum alatum*, *Dipteryx panamensis*), or chemical defenses (*Mucuna boltonii*) against seed predators. Mammal abundances were determined over 3 yrs from open-access motion-detecting camera trap photos. Using semi-permeable mammal enclosures and thread-marked seeds, predation and dispersal by mammals for each seed species were quantified. Abundances of peccaries were up to six times higher than those of agoutis over 3 yrs, but neither peccary nor agouti abundances differed across years. Seeds of *A. alatum* were predominantly dispersed by peccaries, which did not eat *A. alatum* seeds, whereas non-defended and chemically defended seeds suffered high levels of predation, mostly by peccaries. Agoutis did not eat *M. boltonii* seeds. Peccaries and agoutis did not differ in the distances they dispersed seeds. This study shows that seed fates are contingent upon many factors such as seed defenses, frugivore–granivore abundances, and seed-handling capabilities. Mammal–seed interactions are complex; the outcomes of these interactions depend on the inherent characteristics of seeds and their potential dispersers.

Abstract in Spanish is available in the online version of this article.

Key words: agouti; anti-predation defenses; peccary; seed dispersal; seed predation.

ANIMAL-MEDIATED SEED DISPERSAL IS A FUNDAMENTAL PROCESS THAT CAN POTENTIALLY AFFECT seedling establishment, tree distributions, and the maintenance and regeneration of forest ecosystems (Forget 1996, Fragoso 1997, Peres & Baider 1997, Curran *et al.* 1999, Howe & Brown 2001, DeMattia *et al.* 2004). Vertebrates disperse 70–90 percent of woody plant species in tropical forests (Fleming *et al.* 1987). Among vertebrates, mammals act as major seed dispersal agents. Terrestrial mammals may disperse seeds by transporting and depositing them either on the soil surface or by burying them in subsurface caches (scatter-hoarding) (Vander Wall 1990). Dispersed seeds may germinate if they are deposited in suitable microhabitats by mammalian frugivores. Granivorous mammals, however, also consume and destroy many of the seeds they encounter while foraging, acting as seed predators (Asquith *et al.* 1997, DeMattia *et al.* 2004, Jansen *et al.* 2004, Kuprewicz & García-Robledo 2010).

Although it is known that terrestrial mammals affect Neotropical trees positively, via dispersal and hoarding (*e.g.*, Vander Wall 1990, DeMattia *et al.* 2004), and negatively, through predation, herbivory, and seedling trampling (Beck 2005), little is known about the actual net effects that mammals have on seed survival. This scenario can be even more complex because the

effects of terrestrial mammals on different plant life stages may vary among mammal and plant species. Neotropical mammals differ in their abilities to consume and process fruits and seeds due to differences in physiological characteristics such as jaw strength (Kiltie 1982), eating stance, or digestive physiology (Desbiez *et al.* 2009).

Reciprocal selection pressures exist between seed-bearing plants and granivores (Janzen 1980). Plants have evolved seed defenses to deter predation and to enhance seed dispersal. These protective strategies include physical defenses such as thick, hard endocarps that serve as deterrents or barriers to seed consumption, and chemical defenses that render seeds toxic to seed predators (Kiltie 1982, Bodmer 1991, Kuprewicz & García-Robledo 2010). Some mammals can circumvent seed defenses and consume seeds despite physical or chemical protection; however, granivore species vary in their intrinsic abilities to cope with seed defenses (Janzen 1971).

Disparity in relative local frugivore abundances is an extrinsic factor that affects seed encounter rates by animals. Abundances and distributions of terrestrial mammal species vary throughout Neotropical forests and this might affect seed fates within these habitats. Habitat variation, fruiting tree phenologies, food resource patchiness, predator abundances, home range requirements, and anthropogenic effects interact to produce differences in terrestrial frugivorous mammal abundances within

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333

forests (Emmons 1984, Robinson & Redford 1986, Voss & Emmons 1996). Understanding the roles large mammals play in plant reproductive processes is essential because these animals are detrimentally affected by deforestation and hunting by humans (Corlett & Hau 2000, Stoner *et al.* 2007).

Seed dispersers vary in the distances they tend to move seeds (Willson & Traveset 1992). One qualitative measure of seed dispersal effectiveness (*sensu* Schupp 1993) is seed dispersal distance. Seeds benefit from long-distance dispersal by avoiding intense predation pressure near parent plants, decreasing potential competition with conspecifics, and possibly locating microhabitats favorable to seed germination (Howe & Smallwood 1982 and references therein). Terrestrial mammals vary in their likelihoods of dispersing seeds and also in the distances they transport intact seeds. Mammals that have large home ranges will tend to disperse seeds farther than mammals that have small home ranges (Fragoso *et al.* 2003).

In this study, I tested the following hypotheses: (1) seeds on the forest floor are encountered first by peccaries rather than agoutis; (2) more non-defended and chemically defended seeds exposed to peccaries would be destroyed when compared with seeds exposed only to agoutis because peccaries can process toxic seeds via foregut fermentation (Elston *et al.* 2005). I hypothesized that more physically defended seeds would be destroyed by agoutis than by peccaries because agoutis can use their sharp incisors to gnaw through thick endocarps that collared peccaries cannot crush. I also tested two alternate hypotheses concerning mammal seed removal and dispersal kernels: (1) peccaries incidentally disperse seeds farther than agoutis because peccaries cover larger daily foraging ranges than agoutis; or (2) agoutis move seeds they plan to hoard farther from sources than peccaries that incidentally disperse seeds via expectoration; agoutis move hoarded seeds far from sources to escape intense seed predation pressure near the parent plant and to prevent kleptoparasitism of cached seeds by other granivores.

METHODS

STUDY SITE.—The study was conducted from September 2006 through December 2008 in the primary forest at La Selva Biological Station (hereafter La Selva) in Puerto Viejo Sarapiquí, Heredia Province, Costa Rica (10°25'52.610" N, 84°00'12.922" W). La Selva is a tropical lowland wet forest that contains 1600 ha of primary forest, secondary forest, swamps, and tree plantations.

This site receives approximately 4000 mm of rainfall *per annum* with no distinct dry season (McDade *et al.* 1994). Hunting in and habitat fragmentation of the areas surrounding La Selva have resulted in the local extinction of some large terrestrial mammals (*e.g.*, white-lipped peccaries, *Tayassu pecari*).

STUDY SPECIES.—*Mammals.* Collared peccaries (*Pecari tajacu* Linnaeus, 1758; Tayassuidae, Cetartiodactyla) and Central American agoutis (*Dasyprocta punctata* Gray, 1842; Dasyproctidae, Rodentia) are the most abundant terrestrial mammal frugivores within La Selva (Kuprewicz & García-Robledo 2010). Collared peccaries are large (up to 30 kg), terrestrial ungulates that consume fruits and seeds from numerous plant families (Beck 2005, 2006). Collared peccaries range throughout Central America and forage in herds of 2–50 individuals that travel over large home ranges (*e.g.*, 118 ha in a Costa Rican dry forest, McCoy *et al.* 1990). Due to their large body masses and herd sizes, peccaries can substantially modify natural habitats as they perturb soil, destroy seedlings, and consume seeds when foraging (Kiltie 1982, Beck 2005, 2006). As seed predators, peccaries play a significant role in seed survival to germination and subsequent seedling recruitment (Asquith *et al.* 1997). Peccaries cannot masticate or consume some seeds protected by thick-walled endocarps, but due to pregastric fermentation, they can digest many chemically defended seeds (Kuprewicz & García-Robledo 2010).

Central American agoutis are 3–4 kg terrestrial frugivorous rodents found throughout Central America (Reid 1997). *Dasyprocta punctata* are frugivore-granivores that consume and disperse a wide variety of seeds (Smythe 1978). Agoutis bury large seeds singly in shallow caches beneath the soil for retrieval when fruit is scarce and they may serve as the main seed dispersers for some large-seeded tropical trees (Hallwachs 1986, Smythe 1986). Agoutis can gnaw through thick-walled seeds, but they likely cannot consume chemically defended seeds (Kuprewicz & García-Robledo 2010).

Other potential medium large-bodied terrestrial mammal granivores at La Selva include: *Mazama americana*, *Odocoileus virginianus*, *Tapirus bairdii*, *Proechimys semispinosus*, *Heteromys desmarestianus*, *Sciurus* spp., and *Agouti paca*. None of these species, however, were recorded interacting with seeds in my experiments and are therefore not considered in this study.

Plants. For all seed fate experiments, seeds of *Iriartea deltoidea* (Arecaceae), *Socratea exorrhiza* (Arecaceae), *Astrocaryum alatum* (Arecaceae), *Mucuna holtonii* (Fabaceae), and entire fruits of *Dip-*

TABLE 1. Seed and fruit characteristics of all plant species used in seed-tracking experiments. Sample sizes for masses: *Iriartea deltoidea* N = 50, *Socratea exorrhiza* N = 69, *Astrocaryum alatum* N = 104, *Dipteryx panamensis* N = 14, *Mucuna holtonii* N = 50.

Diaspore	Family	Defense	Mass (g) Mean ± 1 SD	Dimensions
<i>I. deltoidea</i>	Arecaceae	None	2.9 ± 0.9	Diameter = 2.4 cm
<i>S. exorrhiza</i>	Arecaceae	None	3.6 ± 0.6	Length = 3 cm, Diameter = 1.75 cm
<i>A. alatum</i>	Arecaceae	Physical (hard endocarp)	25.1 ± 4.5	Length = 6 cm, Width = 4 cm
<i>D. panamensis</i>	Fabaceae	Physical (hard endocarp)	25.2 ± 4.4	Length = 6 cm, Width = 3 cm
<i>M. holtonii</i>	Fabaceae	Chemical (toxic L-dopa)	5.36 ± 0.7	Diameter = 2–3 cm, Thickness = 0.8 cm

terryx panamensis (Fabaceae) were used (Table 1). Due to the large sizes of these five seed species, peccaries and agoutis do not pass these diaspores through their guts intact (endozoochory), rather they grind up seeds prior to ingesting them, which results in complete seed destruction. *Iriartea deltoidea* and *S. exorrhiza* seeds do not possess protection against mammal seed predators either in the form of physical or chemical defenses (Henderson *et al.* 1995). *Astrocaryum alatum* and *D. panamensis* have physical defenses against seed predation in the form of stony endocarps. *Mucuna boltonii* seeds contain high concentrations of the toxic amino acid L-dopa as a chemical defense against seed predation by animals (Daxenbichler *et al.* 1972).

For use in all experiments, ripe fallen fruits were collected from at least 20 individual trees during peak fruiting seasons for each species. Seeds were pooled (by species) and a subset was chosen randomly for use in experiments. Experiments were performed during the months when each respective species was fruiting so as to coincide with the time when ambient abundance of each seed species on the forest floor was highest. Seeds of uniform size and mass with no external evidence of insect infestation or fungal growth were used. To detect insect infestation, each seed was visually inspected for entrance holes indicative of infestation by beetles (Scolytidae or Bruchidae).

RELATIVE ABUNDANCES OF PECCARIES AND AGOUTIS WITHIN LA SELVA.—Camera-trap data from the Tropical Ecology Assessment and Monitoring Network (TEAM Network, <http://www.teamnetwork.org/en/>) were used to determine relative abundances of peccaries and agoutis within La Selva. Between March and June from 2006 to 2008, TEAM deployed pairs of passive infrared motion-detecting camera traps (Reconyx RC55 RapidFire Color IR) at points throughout La Selva to monitor terrestrial mammals (camera point densities for 2006 and 2007: 1 camera point/km², 2008: 1.25 camera points/km²; TEAM Network 2008). All photos were automatically date and time stamped to distinguish unique events.

To collect relative mammal abundance data for 2006, 2007, and 2008, the numbers of individual peccaries or agoutis were counted in each picture taken by one camera at each site in pictures taken at least 20 min apart. Cameras were equally sensitive to peccaries and agoutis (Kuprewicz & García-Robledo 2010). Because no bait was used to lure animals to camera points, I assumed that animals moved completely through the camera focal area within 20 min, preventing re-counting of individual animals within single photographic events. Following this protocol, photographic captures of unique individuals at each trapping site were recorded for each year. Relative abundances of peccaries and agoutis per site per year were compared using a two-way ANOVA.

TIMES TO SEED DEPOT DISCOVERY BY PECCARIES AND AGOUTIS.—To accurately determine the likelihood of seeds on the ground being discovered first by either peccaries or agoutis, digital motion-detecting camera traps (Moultrie GameSpy 2.0) were positioned 1.5 m above seed offers (methods modeled after Jansen &

Ouden 2005). All photos were stamped with times and dates and this information was used to measure the number of days from depot deployment until each mammal species encountered and manipulated seeds within each of the seed depots. Seed detection rates (Kaplan-Meier curves) of peccaries and agoutis were compared for all seed species using log-rank tests.

SEED FATES AND SEED SURVIVAL OVER TIME.—To monitor how peccaries and agoutis affect seed survival over time, individually numbered thread-marked seeds of *I. deltoidea*, *S. exorrhiza*, *A. alatum*, *D. panamensis*, and *M. boltonii* were tracked over periods of 36 d for 3 yrs. For each seed species, locations were selected for seed depot pairs throughout the primary forest separated by minimum distances of 400 m. At each site, two seed depots (separated by 2–4 m) were constructed in a paired design: one depot had a semi-permeable enclosure that excluded peccaries, but allowed agouti entrance and access to seeds within (caged) and the other seed depot had no enclosure and a seed offer available to both peccaries and agoutis (open) (Fig. S1). The open depot contained seeds accessible to all terrestrial mammals; however, only peccaries and agoutis interacted with seeds during this study (according to camera-trap photographs). Seed depot sample sizes for each seed species were $N = 15$ open and $N = 15$ caged treatments except for *S. exorrhiza* where $N = 16$ for each treatment.

Each seed depot within the pair contained nine seeds of a single species arranged in a 3×3 grid; each seed depot pair contained a total of 18 seeds from a single seed species. Peccary enclosures consisted of $1.5 \times 1.5 \times 1$ m (L \times W \times H) galvanized metal fencing sunken and firmly staked into the ground and supported by PVC poles at each corner. I cut one 20×15 cm opening on each side of these enclosures, allowing agoutis and small mammals access to the seeds within, but excluding peccaries (Fig. S1). Each seed depot was outfitted with a digital motion-detecting camera trap to record the identities of seed removing animals interacting with individual seeds both within and outside enclosures. Cameras were attached to nearby trees and located 1.5–2 m aboveground looking down on the seed offers. Because all seeds were uniquely numbered and placed in successive order within each seed grid, I was able to record the species of terrestrial mammal that interacted with each individual seed.

To track seed fates over time and to facilitate seed relocation on the forest floor, a 50-cm length of fluorescent pink nylon twine was attached to each seed. Threads were tied through a single hole drilled in each seed. A 1×2.5 cm uniquely numbered aluminum tag and 10 cm of pink flagging tape were attached to the distal end of the thread. For *M. boltonii* seeds, the drilled hole was filled with melted paraffin to prevent endosperm excavation by ants (Kuprewicz & García-Robledo 2010); based on pilot studies, ants did not attack the other species, so paraffin was not used to fill the holes in these seeds.

Each seed depot was checked every 2 d for 36 d and the forest floor surveyed to recover seeds and strings. The number of seeds removed from sources, fates of recovered seeds (predation, dispersal, hoarding), and seed removal distances were

recorded. A seed detached from a thread indicated an act of predation, whereas a thread still attached to a moved seed located above the soil surface indicated an act of seed dispersal. Seeds cached by agoutis could also be detected as strings remained atop the soil surface attached to buried seeds. Photographs taken by camera traps were used to determine which mammal species removed each individual seed. Failure time analysis (Cox Proportional Hazards model, R Development Core Team 2009) was used to compare the relative rates of seed predation by peccaries and agoutis for each of the five seed species. Wilcoxon matched-pairs tests were used to compare the median numbers of seeds of each species alive after 36 d within and outside of peccary exclosures.

PATTERNS OF SEED REMOVAL AND DISPERSAL BY TERRESTRIAL MAMMAL FRUGIVORES.—To calculate seed removal and dispersal distances, the distances of thread-marked seeds removed from their sources were measured. I refer to removal as animal-mediated seed movement from the source regardless of fate. To determine if peccaries and agoutis exhibit similar seed movement patterns, seed removal and dispersal kernels of peccaries and agoutis were compared for each seed species using Kolmogorov-Smirnov tests. To determine which mammal species disperses seeds farthest, Wilcoxon rank-sum tests compared the median distances of seeds dispersed by peccaries and agoutis for each seed species.

RESULTS

RELATIVE ABUNDANCES OF PECCARIES AND AGOUTIS WITHIN LA SELVA.—Photographs from a total of 16 camera sites in 2006 and 2007 and 20 sites in 2008 showed that the relative abundances of both peccaries and agoutis remained constant from 2006 through 2008. Within each year, however, peccaries were more abundant (up to six times more abundant) relative to agoutis, as indicated by two-way ANOVA (Table 2; Fig. 1).

TIMES TO SEED DEPOT DISCOVERY BY PECCARIES AND AGOUTIS.—For all species, peccaries encountered seed depots significantly faster than agoutis (Fig. 2). Peccaries discovered *I. deltoidea* seeds more quickly than agoutis ($\chi^2 = 10$, $df = 1$, $P < 0.002$; Fig. 2A). Peccaries also were first to find *S. exorrhiza* seeds ($\chi^2 = 25.9$, $df = 1$, $P < 0.001$; Fig. 2B), *A. alatum* seeds ($\chi^2 = 5$, $df = 1$, $P < 0.03$; Fig. 2C), *D. panamensis* fruits ($\chi^2 = 9.2$, $df = 1$, $P < 0.0024$; Fig. 2D), and *M. boltonii* seeds ($\chi^2 = 26.6$, $df = 1$, $P < 0.001$;

TABLE 2. Two-way ANOVA comparing La Selva peccary and agouti abundances (unique photo captures) within and across three consecutive years of study (2006, 2007, 2008). Significant results are shown in bold.

Source of variation	df	Sum of squares	F	P
Year	1	1413	1.74	0.19
Mammal	1	8354	10.31	<0.002
Year × Mammal	1	259	0.32	0.57
Residuals	96	77757		

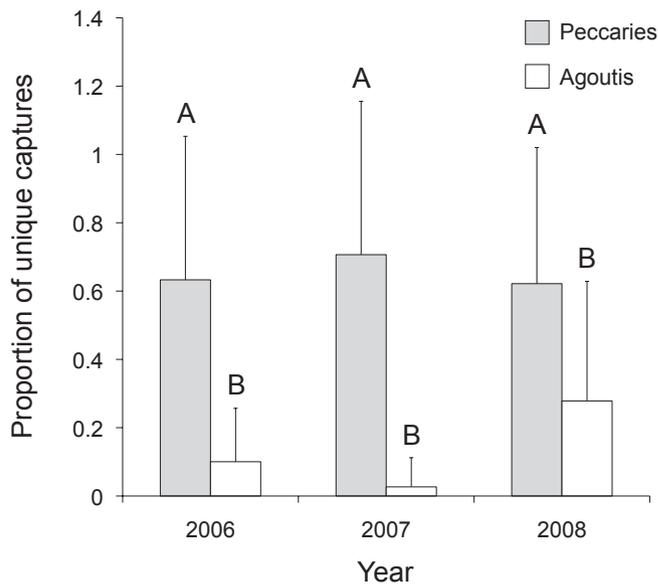


FIGURE 1. Mean proportion of unique photo captures (+1 SD) of collared peccaries (gray bars) and Central American agoutis (white bars) per site per year. Letters group similar categories. Number of sites monitored in 2006 = 16, 2007 = 16, 2008 = 20.

Fig. 2E). At the end of this study, peccaries had encountered 93 percent of *I. deltoidea* seed depots, 100 percent of *S. exorrhiza* depots, 87 percent of *A. alatum* depots, 93 percent of *D. panamensis* depots, and 100 percent of *M. boltonii* depots, whereas agoutis had encountered 60, 13, 60, 40, and 7 percent of these depots, respectively (Fig. 2).

SEED FATES AND SEED SURVIVAL OVER TIME.—Based on photographs taken by cameras at seed depots, peccaries and agoutis were the only terrestrial mammals that interacted with thread-marked seeds. Although pacas (*Agouti paca*), spiny rats (*Proechimys semispinosus*), squirrels (*Sciurus* spp.), and armadillos (*Dasybus novemcinctus*) were observed visiting some seed depots, none of these animals interacted with thread-marked seeds.

Most seeds and strings that were handled by animals were recovered: 139 of 145 displaced *I. deltoidea* seeds and tags (96%), 148 of 151 removed *S. exorrhiza* seeds and tags (98%), 86 of 88 *A. alatum* seeds and tags (98%), 126 of 131 *D. panamensis* fruits and tags (96%), and 135 of 135 *M. boltonii* seed tags (100%).

For all seed species, relative rates of seed predation in open depots were significantly faster than predation rates within peccary exclosures. Species-specific pairwise comparisons of caged and open treatments revealed significant differences in the relative rates of seed predation within and outside of peccary exclosures for *I. deltoidea* ($\chi^2 = 179.2$, $df = 1$, $P < 0.001$), *S. exorrhiza* ($\chi^2 = 275.5$, $df = 1$, $P < 0.001$), *A. alatum* ($\chi^2 = 5.3$, $df = 1$, $P < 0.03$), *D. panamensis* ($\chi^2 = 42.6$, $df = 1$, $P < 0.001$), and *M. boltonii* (no statistical comparison required) (Fig. 3).

For all seed species except *A. alatum*, the median numbers of seeds alive after 36 d were higher for seeds protected from peccaries compared with seeds exposed to peccaries.

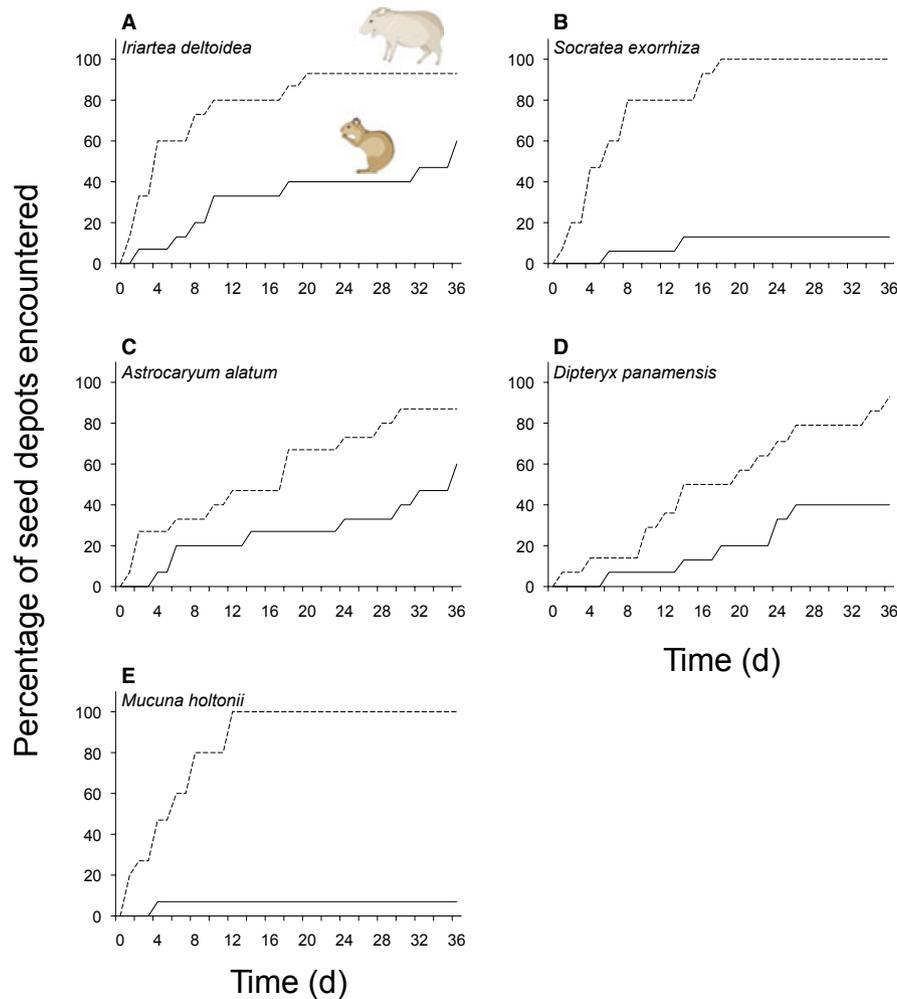


FIGURE 2. Seed depot discovery by terrestrial frugivores. Cumulative percentage of seeds of (A) *Iriartea deltoidea*, (B) *Socratea exorrhiza*, (C) *Astrocaryum alatum*, fruits of (D) *Dipteryx panamensis*, and seeds of (E) *Mucuna holtonii* encountered by peccaries (dashed line) and agoutis (solid line) over 36 d.

Comparisons of caged and open seed depots found significant differences in the median numbers of surviving seeds for *I. deltoidea* ($V = 119$, $P < 0.001$), *S. exorrhiza* ($V = 120$, $P < 0.001$), *D. panamensis* ($V = 75$, $P < 0.005$), and *M. holtonii* ($V = 120$, $P < 0.001$). There was no significant difference in the median number of *A. alatum* seeds alive after 36 d for seeds protected from and seeds exposed to peccaries ($V = 15$, $P = 0.40$); all *A. alatum* seed predation was by agoutis and did not differ within and outside of peccary exclosures because agoutis had equivalent access to all seeds.

PATTERNS OF SEED REMOVAL AND DISPERSAL BY TERRESTRIAL MAMMAL FRUGIVORES.—Within 36-d periods, peccaries had removed 47 percent ($N = 126$) of *I. deltoidea* seeds, 50 percent ($N = 136$) of *S. exorrhiza* seeds, 9 percent ($N = 25$) of *A. alatum* seeds, and 38 percent ($N = 102$) of *D. panamensis* fruits. Agoutis removed 10 percent ($N = 28$) of *I. deltoidea* seeds, 7 percent ($N = 20$) of *S. exorrhiza* seeds, 29 percent ($N = 79$) of *A. alatum* seeds, and 20 percent ($N = 53$) of *D. panamensis* fruits. Neither

peccaries nor agoutis moved *M. holtonii* seeds from their sources; all *M. holtonii* seed predation by peccaries occurred *in situ*. Peccary and agouti seed removal kernels for *I. deltoidea* did not differ significantly in their distributions ($D = 0.23$, $P = 0.16$), whereas comparisons of peccary and agouti seed removal kernels showed significant differences for *S. exorrhiza* ($D = 0.34$, $P < 0.02$), *A. alatum* ($D = 0.42$, $P < 0.003$), and *D. panamensis* ($D = 0.33$, $P < 0.001$) with agoutis tending to move seeds farther from their sources than peccaries (Fig. 4).

Overall, dispersal and hoarding of intact seeds was infrequent within this study. At the end of 3 yrs, peccaries had dispersed 6 percent ($N = 16$) of *I. deltoidea* seeds, 2 percent ($N = 6$) of *S. exorrhiza* seeds, 9 percent ($N = 24$) of *A. alatum* seeds, and 11 percent ($N = 29$) of *D. panamensis* fruits. Agoutis only dispersed 1 percent ($N = 3$) of *I. deltoidea* seeds, 0.4 percent ($N = 1$) of *S. exorrhiza* seeds, 7 percent ($N = 18$) of *A. alatum* seeds, and 3 percent ($N = 8$) of *D. panamensis* fruits. No *M. holtonii* seeds were dispersed by either mammal species. Comparisons of seed dispersal kernels produced by peccaries and agoutis

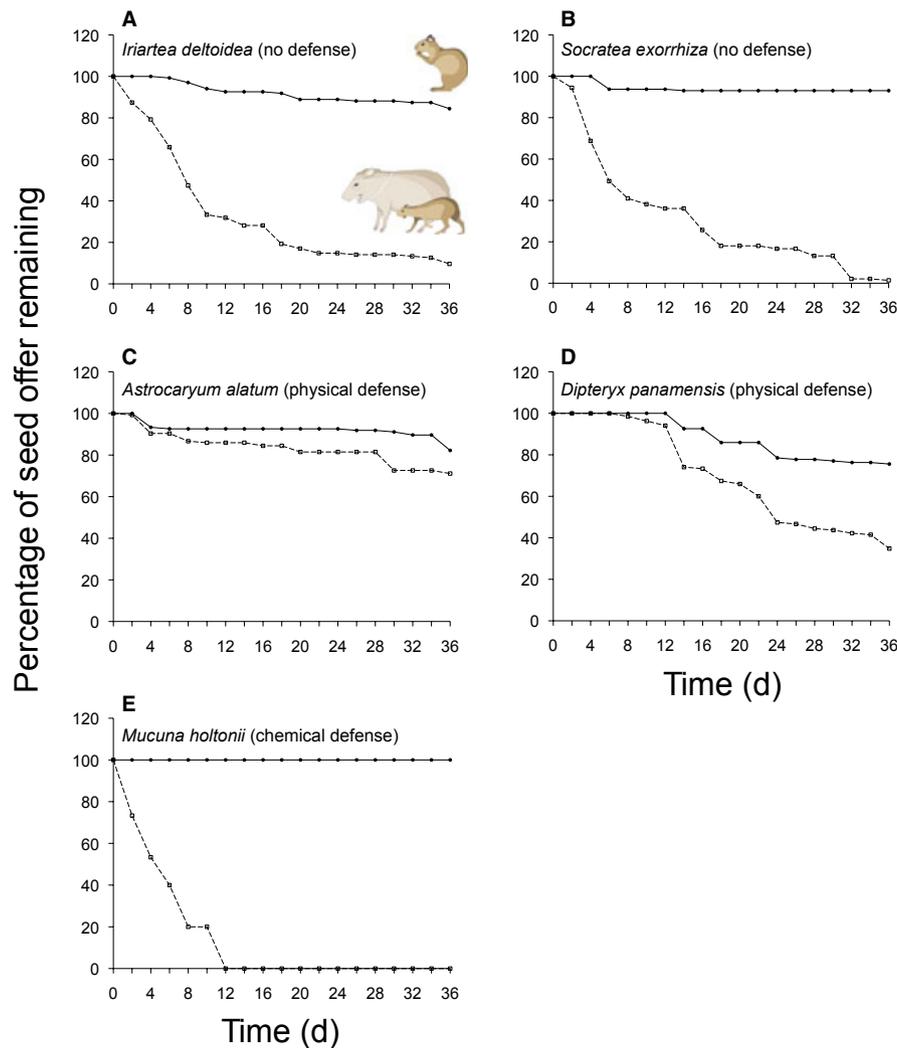


FIGURE 3. Mean percent per depot of surviving seeds of (A) *Iriartea deltoidea*, (B) *Socratea exorrhiza*, (C) *Astrocaryum alatum*, fruits of (D) *Dipteryx panamensis*, and seeds of (E) *Mucuna holtonii* inside (filled circle, solid line) and outside (open square, dashed line) semi-permeable mammal enclosures. Seeds within enclosures were exposed to agoutis only and seeds outside of enclosures were available to all terrestrial mammals (peccaries and agoutis). $N = 30$ seed depots (15 caged, 15 open) for all plant species except *S. exorrhiza*, $N = 32$ depots (16 caged, 16 open).

showed that dispersal distance distributions were not significantly different for any of the seed species (*I. deltoidea*: $D = 0.31$, $P = 0.92$; *S. exorrhiza*: $D = 0.83$, $P = 0.71$; *A. alatum*: $D = 0.17$, $P = 0.91$; *D. panamensis*: $D = 0.41$, $P = 0.25$; Fig. 5). Median distances of seeds dispersed by peccaries and agoutis also did not differ for *I. deltoidea* ($W = 25$, $P = 0.96$), *S. exorrhiza* ($W = 5$, $P = 0.57$), *A. alatum* ($W = 217$, $P = 0.85$), and *D. panamensis* ($W = 78.5$, $P = 0.17$).

DISCUSSION

Peccaries and agoutis are the most abundant terrestrial mammal species at La Selva (TEAM Network, <http://www.teamnetwork.org/en/>). When comparing the relative abundances of peccaries and agoutis within La Selva, peccaries were up to six times more abundant than agoutis from 2006 to 2008. Peccaries produce

larger litters and produce litters more frequently than agoutis, likely contributing to abundance disparities between these species (Smythe 1978, Reid 1997). In addition, white-lipped peccaries (*T. pecari*) have been locally extinct from the Sarapiquí region for approximately 50 yrs. Likely due to the extirpation of white-lipped peccaries and a subsequent release from competition, collared peccaries have increased in number throughout La Selva (McDade *et al.* 1994). It is also worth noting that large predators of peccaries (e.g., *Panthera onca*, *Puma concolor*) are uncommon in La Selva with *P. onca* being especially rare (TEAM Network, <http://www.teamnetwork.org/en/>).

The probability of a seed on the forest floor being found and handled by a peccary is higher than the likelihood of a seed being encountered by an agouti as indicated by shorter times to seed depot discovery by peccaries. Several factors may have contributed to these differences in encounter rates. In addition to

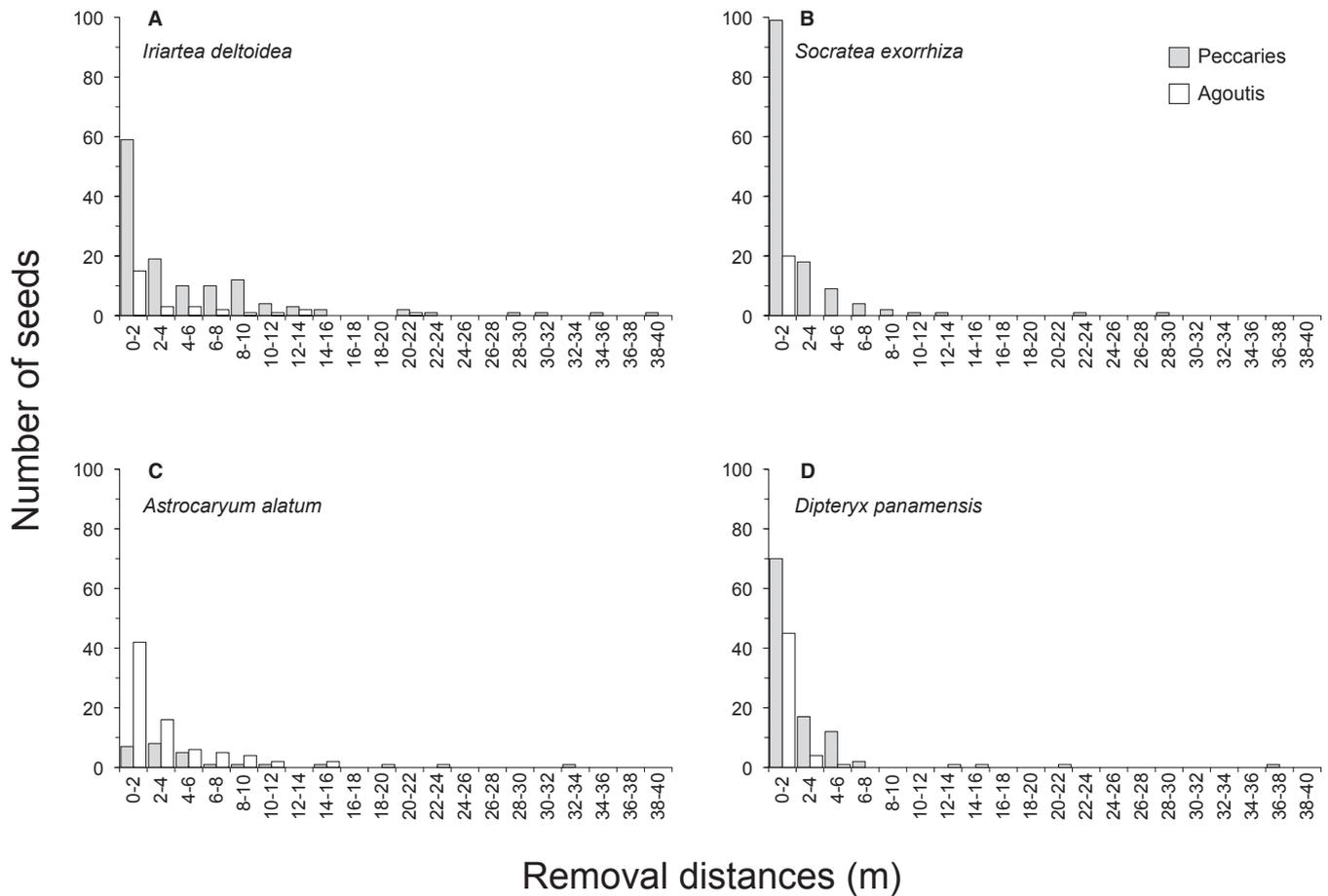


FIGURE 4. Frequency distributions of (A) *Iriartea deltoidea*, (B) *Socratea exorrhiza*, (C) *Astrocaryum alatum*, and (D) *Dipteryx panamensis* seed removal distances by peccaries (gray bars) and agoutis (white bars).

differential abundances, the respective foraging strategies of these mammal species likely affect seed encounter rates. Collared peccaries forage in large groups of 3–15 individuals and occasionally larger, and these cover large foraging areas, enabling peccaries to encounter and consume many recently fallen seeds (Castellanos 1983, Judas & Henry 1999). In contrast, agoutis are solitary foragers that sometimes travel in pairs within their territories (Smythe 1978). In addition, the home ranges of these two mammal species differ greatly and probably contribute to differences in seed encounter rates. Collared peccaries forage within large home ranges varying from 38 ha (Castellanos 1985) to 685 ha (Taber *et al.* 1994), whereas Central American agoutis have much smaller home ranges of 1–4 ha (Smythe 1978, Hallwachs 1986). With agouti home ranges and foraging areas being much smaller than those of peccaries, a seed located on the forest floor is more likely to fall within an area traversed by many peccaries rather than a small territory containing an agouti pair.

Most seeds in this study were first encountered by peccaries and subsequently consumed and destroyed. Ultimate seed fate, however, was contingent on the presence or quality of seed defenses. When protected from peccaries and exposed only to agoutis, most seed species had high percentages of survival

(76–100%). This result indicates that agoutis do not kill the majority of seeds they encounter and peccaries predominantly negatively affect large seed survival through predation. Paine and Beck (2007) found that, in Cocha Cashu Peru, peccaries did not significantly affect seedling recruitment (either positively or negatively), whereas agoutis negatively affected seed and seedling survival. These differences may be attributable to the particular floristic and faunal characteristics that distinguish the forests of Cocha Cashu and La Selva.

Contrary to expectation, peccaries destroyed a higher proportion of physically defended *D. panamensis* seeds than agoutis. These findings do, however, corroborate previous research (Beck 2005 and references therein). *Dipteryx panamensis* seeds are protected by a thick, stony endocarp, but peccaries were able to open mature *D. panamensis* fruits and consume seeds. When *D. panamensis* fruits have recently fallen to the forest floor, the suture encircling the endocarp is tightly sealed and peccaries cannot break them, but as fruits age on the ground, this suture weakens, the stony endocarp dehisces to allow radicle and plumule emergence, and peccaries can exploit this weakened seam to open fruits (Enders 1935). Physical defense against seed predation for *D. panamensis* is ephemeral as seeds are protected from peccary

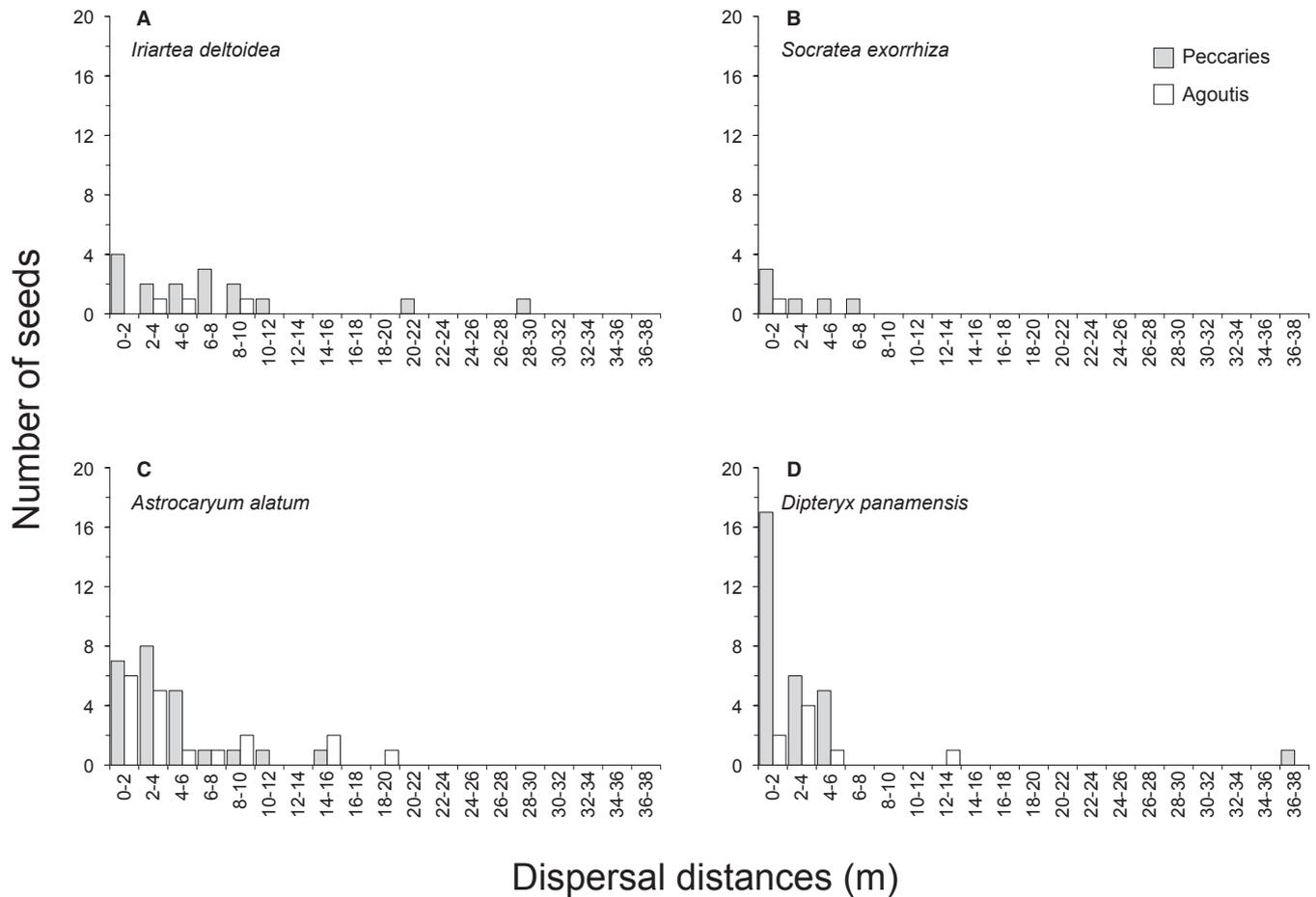


FIGURE 5. Frequency distributions of (A) *Iriartea deltoidea*, (B) *Socratea exorrhiza*, (C) *Astrocaryum alatum*, and (D) *Dipteryx panamensis* seed dispersal distances by peccaries (gray bars) and agoutis (white bars).

predation only when freshly dropped from parent trees. Agoutis, however, can open *D. panamensis* fruits at any stage of ripeness by gnawing directly through the endocarp. Post-dispersal hoarding by agoutis may allow *D. panamensis* fruits to escape seed predation by peccaries, especially if there are high levels of ambient fruit available to satiate seed predators and prevent predation of cached seeds by agoutis (Forget 1993, Ruiz *et al.* 2010).

Peccaries possess complex stomachs capable of foregut fermentation, allowing them to consume toxic seeds that agoutis cannot (Elston *et al.* 2005, Kuprewicz & García-Robledo 2010). All *M. boltonii* seeds within peccary enclosures survived to the end of the study, indicating that agoutis did not consume any seeds of this species, whereas peccaries consumed and destroyed all of the *M. boltonii* seeds they could access.

The only seeds protected from predation by peccaries were *A. alatum*. Peccaries did not consume any seeds of this physically defended species; all predation of *A. alatum* seeds was by agoutis. The bite force provided by collared peccary jaws is apparently not strong enough to break through the endocarp of *A. alatum* seeds. Due to their inability to consume *A. alatum*, peccaries may act as incidental seed dispersers (Beck 2005). In other studies in

Peru and Panama, collared peccaries have been observed cracking endocarps and consuming seeds of *A. murumuru* (= *macrocalyx*) and *A. standleyanum* (Smythe 1978, Kiltie 1982, Beck 2006). These *Astrocaryum* species may possess thinner endocarps than *A. alatum* at La Selva, allowing *A. murumuru* and *A. standleyanum* to be exploited by collared peccaries.

All *A. alatum* seed predation within this study was by agoutis. *Astrocaryum alatum* seed survival within and outside peccary enclosures did not differ, indicating equivalent discovery and handling of seeds by agoutis in both treatments. Physical defenses did not deter seed predation by agoutis that gnawed through to *A. alatum* seeds by repeatedly rasping the endocarp with sharp incisors.

In this study, levels of seed dispersal and hoarding were low (only 10 hoarding events were observed). This low hoarding frequency may be attributed to the lack of seasonality within La Selva and resultant high levels of year-round ambient fruit abundance. Also, seeds may not be found and hoarded by agoutis because peccaries encounter and destroy most seeds before agoutis can locate them. Although scatter-hoarding of seeds by agoutis enhances seed survival and germination (Forget 1993, 1994,

Brewer & Rejmanek 1999), this phenomenon may not significantly contribute to tree recruitment and propagation within La Selva.

With regard to seed dispersal, peccaries moved most seeds within 10 m of the source with a few long-distance dispersal events (>30 m). Agoutis also moved seeds mostly short distances and long-distance dispersal by this species was rare. These results are comparable to other studies involving seed dispersal by peccaries and agoutis (Fragoso 1997, but see Jansen *et al.* 2012 for long-distance dispersal by agoutis). Contrary to my hypotheses, peccaries and agoutis exhibited no differences in seed dispersal kernels or the median distances they dispersed intact, viable seeds. These mammals are equally effective seed dispersers with regard to distance, although agoutis may provide more effective qualitative dispersal by hoarding some seeds below the soil surface, effectively hiding seeds from vertebrate and invertebrate seed predators (Fragoso 1997, Silvius 1999).

Seeds with either no defenses or chemical defenses against mammal seed predation face high predation pressure within La Selva because peccaries are locally abundant relative to other terrestrial mammals. In contrast, peccary populations are greatly reduced or locally extinct in the hunted, fragmented areas surrounding La Selva. Extirpation of granivorous megafauna has resulted in the proliferation of trees usually regulated by seed predation (Silman *et al.* 2003, DeMattia *et al.* 2004). Loss of peccaries and agoutis from forest fragments surrounding La Selva has resulted in reduced predation of *D. panamensis* seeds and a dramatic increase in *D. panamensis* seedlings (Hanson *et al.* 2006). With large frugivorous mammals removed from these fragments, seed dispersal services provided by small rodents and bats may contribute significantly to local forest community structure and composition (Melo *et al.* 2009).

In conclusion, relative mammal abundances, intrinsic traits of granivores, and the traits of the seed species they consume interact to produce variable seed fate outcomes. La Selva's high local peccary abundance has far-reaching implications for seed survival and, ultimately, tree propagation. Peccaries encounter seeds on the forest floor quickly and consume and destroy a majority of the seed crop. Chemically defended seeds are effectively protected from agoutis and other granivorous rodents, but peccaries can tolerate seed toxins (*e.g.*, L-dopa). Peccaries may disperse hard-walled seeds incidentally, potentially leading to a proliferation of trees that produce seeds encased in hard endocarps. Although peccaries and agoutis differ in home ranges and foraging techniques, they produce similar seed shadows at La Selva and other Neotropical sites. The seed dispersal and predation behaviors of terrestrial Neotropical mammals are complex and have the potential to dramatically affect the forests in which they occur.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Diagram depicting seed depot pairs (caged treatment, A; open treatment, B) used in seed fate experiments.

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