Small rodents as significant dispersers of tree seeds in a Neotropical forest

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Abstract. Through seed dispersal and predation, terrestrial mammals should be an important component of the mechanisms that determine patterns of tree recruitment in tropical forests. Despite their great abundance and ubiquity in Neotropical forests, small rodents as seed predators and dispersers remain largely forgotten. To investigate the fates of seeds in a hunted primary forest in Belize, we tagged seeds of *Astrocaryum mexicanum* (*Palmae*), *Ampelocera hottlei* (*Ulmaceae*), and *Pouteria sapota* (*Sapotaceae*) and placed them into open plots, exclosures accessible only to small mammals, and exclosures accessible to medium-sized and small mammals. The exclosure experiments and fates of the seeds show that the spiny pocket mouse, *Heteromys desmarestianus* (*Heteromyidae*), was the dominant handler of seeds of the first two species and also removed a significant proportion of the very large-seeded *Pouteria*. Most of the seeds were killed immediately upon removal, but many of the seeds (3-18%) of the first two species were scatterhoarded (dispersed and buried in the soil) by *Heteromys*. Some of the scatterhoarded seeds (29%) remain buried and therefore protected from predation by other animals. Agoutis (*Dasyprocta punctata*), a caviomorph rodent, buried 13 % of the seeds of *Pouteria*, and *Heteromys* consumed and dispersed but did not bury *Pouteria* seeds. Results of this study support predictions by some researchers that small rodents are dominant terrestrial granivores in Neotropical forests. The role of small rodents as seed dispersers, however, has never been fully appreciated.

Keywords: *Ampelocera*; *Astrocaryum;* Belize; Forest recruitment; *Heteromys desmarestianus*; *Pouteria*; Scatterhoarding; Seed dispersal.

Nomenclature: Emmons & Feer (1997); Williams (1977).

Introduction

Terrestrial mammals as secondary seed dispersers and seed predators have begun to receive attention as concerns have been raised over the effects of hunting of mammals on tree diversity in tropical forests (Howe 1984; Emmons 1989; Redford 1992; Terborgh 1992; Chapman & Chapman 1995; Brewer et al. 1997). Tree seed dispersal and predation, considered to be major ecological forces in the structuring and maintenance of diversity in tropical forest communities and the evolution of plants (Janzen 1969, 1971; Howe & Smallwood 1982; Fenner 1985), bestow upon mammals powerful roles in these communities. In fact, the rise of modern tropical forests and the dominance of angiosperms has been attributed in part to the radiation of seed-dispersing mammals and birds in the late Cretaceous/early Tertiary (e.g. Tiffney & Mazer 1995).

Different spatial, temporal and species-specific patterns of seed removal are predicted to have substantial consequences for species distributions, patterns of plant diversity, and community structure (e.g. Janzen 1970, 1971; Howe & Smallwood 1982). Yet, as Forget (1991) pointed out, seed removal is often assumed to mean seed predation (See e.g. Myster 1997). Few studies have actually tracked the fates of removed seeds in the tropics and attempted to quantify the relative amounts of predation and secondary dispersal (but see Hallwachs 1986; Asquith et al. 1997; Forget et al. 1998 and references therein).

Rodents have only recently begun to be investigated as seed predators and dispersers in the Neotropics, although large rodents have been the focus of investigation (e.g. Hallwachs 1986; Smythe 1989). Very little is known about the role of small rodents in seed survival and fates (but see Janzen 1982; Forget 1991; Hoch & Adler 1997) despite their ubiquity and high density in Neotropical forests (Robinson & Redford 1986; Emmons & Feer 1997) and relatively high energetic requirements (e.g. Fleming 1977). While the importance of large rodents (i.e. *Dasyproctidae*) as seed dispersers has been emphasized, some biologists have predicted that small rodents may indeed be significant seed predators and dispersers in the Neotropics (Coates-Estrada & Estrada 1988; Forget 1991; Terborgh & Wright 1994; Adler 1995; Hoch & Adler 1997; Sánchez-Cordero & Martínez-Gallardo 1998). The objectives of this study are to discern patterns of seed removal and test whether or not small rodents dominate the terrestrial removal and fates of seeds of three species of tropical trees, *Astrocaryum mexicanum* (*Palmae*), *Ampelocera hottlei* (*Ulmaceae*), and *Pouteria sapota* (*Sapotaceae*), in a lowland moist forest in Belize.

Methods

Study site and species

Experiments were conducted in the Bladen Nature Reserve (BNR) in the Maya Mountains, Belize, from July 1996 to November 1997. The BNR encompasses 350 km² of hills and narrow valleys of the Bladen Branch watershed, with surrounding hills from 300 - 1000 m a.s.l. The eastern BNR has an annual rainfall of 2500 - 3000 mm, with a pronounced dry season from March through May. Mean monthly minimum and maximum temperatures are 23.4 °C and 29.6 °C, respectively. The study area is in the eastern part of the reserve (16°34'N, 88°43'W, at ca. 45 m a.s.l.) in a lowland, evergreen seasonal tropical forest (Beard 1944) on alluvium over limestone.

The lowland forest is 30 - 40 m tall. Tree diversity (individuals >10 cm DBH) in the mature-phase forest of the study area is 80 - 100 species and 330 - 360 individuals/ha (Brewer unpubl.). Common species include:

Herb layer: *Selaginella umbrosa*; *Araceae* and *Marantaceae*;
Understory: *Astrocaryum mexicanum* (*Palmae*) and *Protium* spp. (*Burseraceae*);
Subcanopy and canopy: *Attalea cohune* (*Palmae*) and *Ampelocera hottlei* (*Ulmaceae*);
Canopy trees: *Quararibea funebris* (*Bombacaceae*), *Mortoniella pittieri* (*Apocynaceae*), *Spondias* spp. (*Anacardiaceae*), *Guarea* spp. (*Meliaceae*), *Dialium guianense* (*Leguminosae*) and some *Sapotaceae*.

The forest has not been logged in recent times. Like most of Central America, however, the study area is heavily hunted, and medium and large terrestrial mammals occur there at low densities (Brewer unpubl.).

Three tree species were used in the seed removal and fate experiments (Table 1).

Astrocaryum mexicanum (e.g. Pinero & Sarukhán 1982; Eguiarte et al. 1993) is monoecious and is the most abundant tree in the study area (503 ind./ha). *Astrocaryum* is abundant in lowland wet forests from southern Mexico to northern Nicaragua (Henderson et al. 1995). Fruiting individuals can be found throughout the year, but fruits are most abundant during the mid-wet season (September - November) and least abundant during the dry season. The fruits of *Astrocaryum* fall beneath the parent tree and are consumed by a wide variety of mammals including small and large rodents, and larger mammals such as peccaries (*Tayassu* spp.) (pers. obs.).

Ampelocera hottlei (*Ulmaceae*) is a common, medium-sized, subcanopy to canopy tree which produces many small, subglobose, fleshy drupes during mid-dry season (April). The fruits/seeds are eaten in the canopy mostly by birds, kinkajous (*Potos flavus*), and probably squirrels (pers. obs.). Large and small rodents have been observed feeding on the ground beneath fruiting trees of *Ampelocera*.

Pouteria sapota (*Sapotaceae*) is a fairly common large, canopy tree that fruits abundantly from December to June at the study site. The large, fleshy fruits (10 - 20 cm long) contain 1 - 4 large seeds and are eaten by tayra (*Eira barbara*), monkeys (*Ateles geoffroyi* and *Alouatta pigra*), kinkajous, and squirrels (*Sciurus* spp.) (pers. obs.). The seeds are eaten on the ground by caviomorph rodents (*Agouti paca* and *Dasyprocta punctata*), squirrels, small rodents, and probably by peccaries.

Seed removal and fate experiments

We established exclosure plots and open control plots in two sites, A and B, of similar elevation, at 350 m distance and located ca. 400 m and 50 m, respectively, from the BNR's major river. Different types of mammals were allowed access to tree seeds. The exclosures, 2 m × 2 m × 1 m, were of hardware cloth (6 mm mesh) supported by PVC stakes at the corners and middle of the sides, and of three types:

(1) 'impermeable', i.e. completely enclosed along the sides and at the base (where flashing weighted with rocks prevented animals from digging into the exclosure plots) but with the tops open and were potentially accessible to climbing rodents;
(2) permeable to small mammals with an open top and seven 6 cm × 7 cm openings at the base of each side;
(3) exclosures permeable to small and medium-sized mammals with an open top and three 30 cm × 30 cm openings per side.

Open plots were marked with four PVC stakes and allowed access by all size classes of animals.

Three replicates of the open plot and each type of exclosure were established at each site in 1996. Two additional replicates of exclosures and open plots were added at each site in early 1997 (total of 10 each in the study area). The exclosures and open plots were placed randomly ca. 20 m apart in each site. Impermeable, permeable to small mammals, and open plots were used in all experiments with all three seed species. Only the first two *Astrocaryum* experiments (wet season 1996, dry season 1997) included the exclosure type permeable to small and medium-sized mammals.

The seeds used in the experiments were tagged such that their fates could be followed when they were removed. The seed tagging method used in this study is a modification of a method by Hallwachs (1986) in the investigation of seed fates. Fruits/seeds were threaded through the seed coat (or apical pericarp for *Astrocaryum*)

Table 1. Seed characteristics of the species used in the removal and fate experiments (mean ± SD). Fruits/seeds were collected on the ground for *Ampelocera* and *Pouteria* and from the tree in *Astrocaryum*, ≥ 50 m away from the experimental sites. Measurements for *Astrocaryum* are of fruits. *Weight of *Ampelocera* from Ibarra-Manríquez & Oyama (1992).

Species	Length (cm)	Weight (g)	Peak fruiting period
Astrocaryum mexicanum	4.7 ± 0.5	14.7 ± 4.6	Wet season: Aug/Feb
Ampelocera hottlei	1.3 ± 0.5	0.67*	Dry season: April/May
Pouteria sapota	7.9 ± 1.6	30 - 60	Dry season: Feb/June

with 2 mm × 150 cm white dacron tags (Izorline, Gardena, California) (60 cm tags were used for *Astrocaryum* in 1996) and placed inside the exclosures and open plots and monitored every one to six days. In most of the experiments, 50 % of the fruits/seeds placed in the exclosures were threaded with the tags and one-half of the fruits were left untagged in order to test for the effect of tagging on removal. Our initial experiments with shorter tags (60 cm) had low recovery rates of removed seeds. We later learned that this low recovery was due to small rodents taking the seeds deep into burrows. Therefore we used longer tags (1.5 or 2 m) in subsequent experiments. In addition to long tags, frequent monitoring of tagged seeds is essential to the success of this method since even the longer tags were pulled into the burrows after only one to four days (Fig. 1). (See Forget et al. 1998 for further discussion of this and other methods).

During all of the removal experiments, when seeds were missing from an exclosure, careful searches for the missing tags were conducted up to 30 m radius from the experimental seed source. Distance moved and fate of the recovered seeds were recorded. Removal of fruits/ seeds from exclosures and open plots was analysed using repeated measures ANOVA (SuperANOVA v. 1.11 1991) with plot (exclosure) type and site as the main effects after angular transformation of the proportions of fruits/seeds removed data.

Removal experiments were conducted for *Astrocaryum* in the 1996 wet season (*n* = 15 fruits/plot, all tagged) and 1997 wet and dry seasons (*n* = 16 fruits/plot, one half tagged). The first experiment began in the beginning of the dry season (February) and was monitored for 107 days. The second experiment began in the wet season (August) and was monitored for 36 days. Removal experiments were also conducted with *Ampelocera* (*n* = 20 seeds/plot, one half tagged) and *Pouteria* (*n* = 5 tagged seeds/plot) seeds during the dry and wet seasons of 1997. These were monitored for 51 days.

Small mammal trapping

In the wet season (August) of 1997, 44 16 cm × 5 cm × 5 cm Tomahawk (single door, wire mesh) traps were placed in one 4 × 11 grid per site with 15 m spacing between traps. Traps were baited with 10 *Astrocaryum* fruits during the darkest phase of the lunar cycle (Emmons 1982) for seven nights (308 trap nights/site) and checked at 6.00 and 17.30 h each day. Mammals caught were given unique fur-clipping marks and were sexed and weighed.
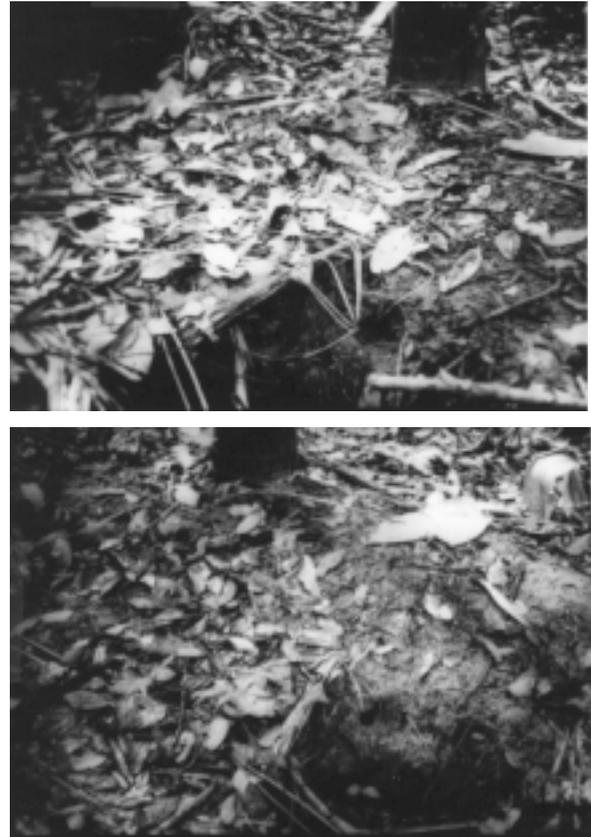

Fig. 1. a. Seed/fruit tags (100-200 cm length) protruding from the entrance to a burrow of the small rodent *Heteromys desmarestianus* during a pilot study to determine optimal seed tag length using tagged *Astrocaryum mexicanum* nuts. **b.** The same burrow entrance two days later. Tags are often pulled completely into the burrows after 1-3 days.

Results

Seed/fruit removal

Exclosures open at the top but without openings at the base experienced no fruit removal during any of the experiments. Arboreal and scansorial mammals such as squirrels are therefore assumed to be unimportant in the removal of fruits/seeds from the exclosure plots, and the open-top type of exclosure plot are not represented in the following figures or analyses.

In all experiments, exclosure plots did not differ significantly from open plots in terms of removal rates (but see *Pouteria* below) nor were there significant differences between exclosure types (Tables 2 and 3, Fig. 2). Furthermore, the fates of the seeds very often revealed the size class of the animal that took any given seed: tags which were moved and trailed under very low branches, through small openings in the vegetation, under logs, etc. could only have been moved by small
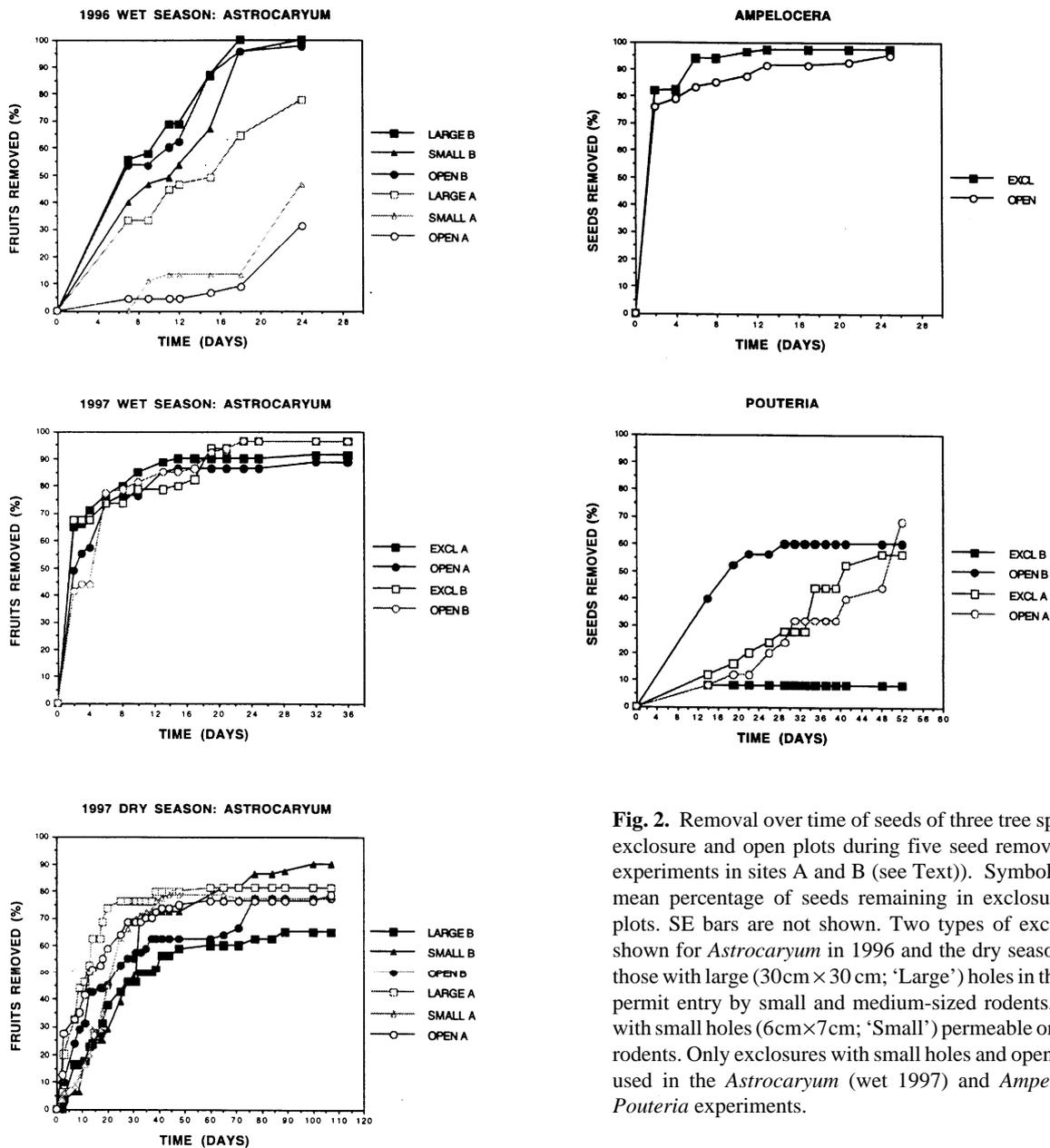
1996 WET SEASON: ASTROCARYUM

1997 WET SEASON: ASTROCARYUM

1997 DRY SEASON: ASTROCARYUM

AMPELOCERA

POUTERIA

Fig. 2. Removal over time of seeds of three tree species from exclosure and open plots during five seed removal and fate experiments in sites A and B (see Text)). Symbols represent mean percentage of seeds remaining in exclosure or open plots. SE bars are not shown. Two types of exclosures are shown for *Astrocaryum* in 1996 and the dry season of 1997: those with large (30cm × 30 cm; 'Large') holes in their sides to permit entry by small and medium-sized rodents, and those with small holes (6cm×7cm; 'Small') permeable only to small rodents. Only exclosures with small holes and open plots were used in the *Astrocaryum* (wet 1997) and *Ampelocera* and *Pouteria* experiments.

animals (see also fates below). Given the telltale signs of small rodents and that the removal rates and fates of *Astrocaryum* and *Ampelocera* fruits/seeds were nearly identical between the exclosure and open plots, seed removal must have been performed almost exclusively by small rodents. Finally, no significant effect of tagging on removal rate was detected.

Removal rates of seeds were highest for *Ampelocera* followed by *Astrocaryum* and *Pouteria* (Fig. 2). There were both site and seasonal effects in seed removal for *Astrocaryum*, but not for *Ampelocera* (Tables 2 and 3, Fig. 2). Removal of *Astrocaryum* fruits during the wet season of 1996 was significantly lower at site A than site B

(Table 2, Fig. 2). This site effect was reversed in the dry season of 1997, although the effects were not statistically significant ($p = 0.06$, Table 2); site A had higher removal rates than site B (Fig. 2). A significant effect of site was not detected during the 1997 wet season. The rate of removal of *Astrocaryum* fruits during the wet season of 1997 was nearly four times the removal rate in the dry season, and final percent removed was also higher in the wet season (Fig. 2).

Significantly more seeds of *Pouteria* were removed from open plots by large than small rodents ($t = 4.208$, $df = 13$, $p = 0.001$) (using teeth marks on the seeds as an indicator of rodent size), suggesting that agoutis handle

Table 2. Repeated measures ANOVA of removal of *Astrocaryum mexicanum* from separate experiments. Factors potentially affecting seed removal include site (two sites, 400 or 50 m to the nearest major river) and plot type ('plot'; exclosures and open plots; see Methods).

Source of variation	df	ss	ms	F	p
Astrocaryum mexicanum 1996 Wet Season					
Site	1	12.051	12.051	19.808	0.0008
Plot	2	2.673	1.337	2.197	0.1538
Site × plot	2	1.032	0.516	0.848	0.4524
Subjects within groups	12	7.300	0.608		
Time (days)	7	15.937	2.277	38.906	0.0001
Time × site	7	2.519	0.360	6.150	0.0001
Time × plot	14	0.703	0.050	0.858	0.6054
Time × site × 4.074 plot	14	0.265	0.019	0.323	0.9894
Time × subjects (groups)	84	4.915	0.059		
Astrocaryum mexicanum 1997 Dry season					
Site	1	4.698	4.698	3.835	0.0619
Plot	2	0.144	0.072	0.059	0.9432
Site × Plot	2	2.960	1.480	1.208	0.3163
Subjects within groups	24	29.404	1.225		
Time (days)	28	93.182	3.328	89.027	0.0001
Time × site	28	1.632	0.058	1.559	0.0340
Time × plot	56	4.963	0.089	2.371	0.0001
Time × site × plot	56	0.780	0.014	0.373	1.0000
Time × subjects (groups)	672	25.120	0.037		
Astrocaryum mexicanum 1997 Wet season					
Site	1	0.006	0.006	0.004	0.9524
Plot	1	0.181	0.181	0.110	0.7445
Site × plot	1	0.001	0.001	0.001	0.9820
Subjects within goups	16	26.364	1.648		
Time (days)	15	39.184	2.612	52.770	0.0001
Time × site	15	0.328	0.022	0.442	0.9649
Time × plot	15	0.929	0.062	1.251	0.2349
Time × site × plot	15	0.098	0.007	0.132	1.0000
Time × subjects (groups)	240	11.881	0.050		

Table 3. Repeated measures ANOVA of removal of *Pouteria sapota* and *Ampelocera hottlei* from separate experiments. Factors potentially affecting seed removal include site (two sites, 400 or 50 m to the nearest major river) and plot type ('plot'; exclosures and open plots, see Methods).

Source of variation	df	ss	ms	F	p
Pouteria sapota Wet season 1997					
Site	1	0.030	0.030	0.010	0.9205
Plot	1	7.133	7.133	2.447	0.1373
Site × plot	1	10.661	10.661	3.657	0.0739
Subjects within groups	16	46.637	2.915		
Time (days)	13	9.741	0.749	18.837	0.0001
Time × site	13	2.879	0.221	5.566	0.0001
Time × plot	13	0.864	0.066	1.671	0.0690
Time × site × plot	13	1.206	0.093	2.332	0.0065
Time × subjects (groups)	208	8.274	0.040		
Ampelocera hottlei Dry season 1997					
Site	1	0.166	0.166	0.293	0.5956
Plot	1	0.608	0.608	1.072	0.3158
Site × plot	1	0.020	0.020	0.036	0.8516
Subjects within groups	16	9.066	0.567		
Time (days)	11	36.624	3.329	171.501	0.0001
Time × site	11	0.435	0.040	2.039	0.0273
Time × plot	11	0.160	0.015	0.749	0.6905
Time × site × plot	11	0.189	0.017	0.883	0.5581
Time × subjects (groups)	176	3.417	0.019		

Pouteria seeds first. Nevertheless, small rodents were capable of removing and consuming *Pouteria* seeds as rapidly as agoutis in site A (Fig. 2). However, there was an interaction effect between site and plot type (open vs. exclosure) for removal of *Pouteria*, albeit not statistically significant (Table 3); exclosures at site B had much lower removal rates and appeared to level off very early compared to the exclosures at site A (Fig. 2). Therefore, removal rates by small rodents of this seed species appear to be influenced by site.

Fates of seeds/fruits

Seeds removed from exclosures could have one of four fates. The seeds could be (1) moved on the surface of the forest floor, (2) moved on the surface and buried (by scatterhoarding), (3) taken underground into small mammal burrows, or (4) 'lost' and their true fates would be unknown. All seeds not buried were considered to be killed because they were consumed on the spot, were peeled and missing and therefore assumed to be dead (peeled seeds left by rodents desiccate or rot and are eaten by ants), or were taken to places where they would likely die (deep burrows, logs, palm leaf sheaths, etc.).

Although most seeds were killed during the experiments, some of the seeds/fruits were buried away from the exclosures and open plots (Fig. 3, Table 4). The seeds/fruits of *Astrocaryum* and *Ampelocera* were buried by small rodents, as indicated by teeth marks on the seeds, paths taken by the mammal (as indicated by the seed tag), or by their fate. For example, very often when a group of seeds were removed from an exclosure one night and buried, some other seeds of this group were taken into nearby small-rodent burrows the same night. Furthermore, many seeds that were buried and later excavated (see below) were taken into these burrows.

Seeds of other tree species were also observed to be buried by small rodents. Two caches (of six thoroughly investigated) of the experimental *Ampelocera* seeds contained seeds of other tree species in them, including *Manilkara* spp. (*Sapotaceae*), *Bactris mexicana* (*Palmae*), and a small seeded species of *Pouteria* (*Sapotaceae*). In a pilot study in 1996, tagged seeds of *Brosimum alicastrum*

Table 4. Comparison of the distances of seeds moved in four independent experiments. Data are mean distances in m with standard error in parentheses. Means sharing the same letter within a column are not significantly different ($p > 0.05$, Scheffe's test).

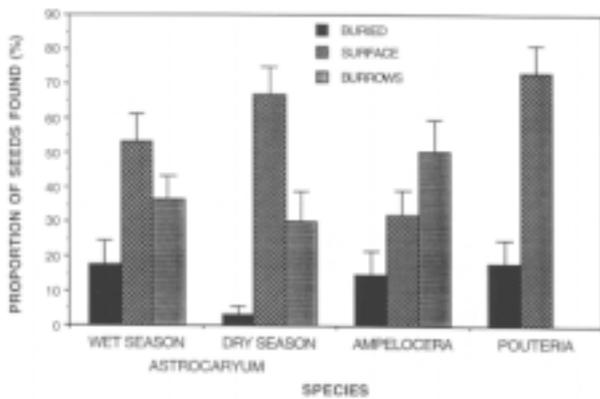|	Species			
	Astrocaryum		*Ampelocera*	*Pouteria*
Seed fate	Wet season	Dry season	Wet season	Dry season
Surface	3.9 (0.64)[a]	2.6 (0.30)[a]	3.1 (0.66)[a]	4.1 (0.60)[a]
Buried	4.3 (0.59)[a]	3.7 (1.74)[a,b]	4.3 (0.52)[a]	14.8 (7.6)[b]
Burrows	6.7 (0.68)[b]	4.0 (0.72)[b]	8.5 (0.61)[b]	-

Fig. 3. Fates of fruits/seeds that were removed from open and exclosure plots during four removal and fate experiments. Mean percent (+ SE bars) of seeds found by the authors are represented. Seeds were moved on the surface (into or under logs, at the base of tree buttresses, under piles of duff, etc.) of the forest floor, buried in the soil and/or leaf litter, or moved into small rodent burrows. *Pouteria* burial was only by agoutis.

(*Moraceae*) were also found buried in a manner consistent with that of small rodents.

The fruits/seeds of *Ampelocera* and *Astrocaryum* were found to be most often buried in the soil, occasionally only half-buried in the soil, and almost always covered by 1 - 3 cm of soil and/or leaf litter. (Depths were estimated based on average seed sizes; exact depths were not measured for all but a few caches in order to avoid disturbing the seeds and potential cues for recovery.) The percentage of *Astrocaryum* fruits buried in the wet season of 1997 (Table 5) was much higher than in 1996 (6.3 % of those removed per plot). Shorter tags were used in 1996, however, and the percent seeds found was much lower than in 1997.

A significantly greater proportion of *Astrocaryum* fruits were buried in the wet than dry season (paired t = 2.21, df = 19, p = 0.04). All of the buried seeds/fruits of *Ampelocera* and *Astrocaryum* were excavated in the dry season, and in the wet season, some fruits of *Astrocaryum* and *Pouteria* were still buried at the end of the experiment (Table 6). Buried seeds/fruits that were later excavated were all eaten on the forest floor or taken into burrows. Often *Pouteria* seeds buried by agoutis were repeatedly excavated, partly eaten, then reburied.

In the experiment with *Pouteria*, no seeds removed from the exclosures were buried: only large rodents apparently buried the *Pouteria* seeds (ca. 1 - 3 cm deep and covered with soil). Proportions of fruits/seeds removed and buried did not differ significantly between open plots and exclosures for *Ampelocera* and *Astrocaryum*.

Artificial burial does not appear to enhance germination of *Astrocaryum* in the field, but it greatly improves survivorship of seeds (Brewer & Rejmánek, unpubl.).

Table 5. A comparison of the fates of seeds handled by large and small rodents in experiments in Neotropical forests. Seeds dispersed beneath litter or soil ('Cached') or eaten ('Killed') are expressed as mean percent of removed seeds *found by the authors*. '?' = % of removed seeds not found by the authors.

Terrestrial disperser	Tree species		Cached (%)	Killed (%)	? (%)
Dasyproctidae[1]	*Vouacapoua americana* (4.9 cm, 33 g)		67 - 71	29 - 33	3 - 49
Proechymys[2] (23 - 100 % of removal)	*Astrocaryum paramaca*		69	7	NA
			0	100	NA
& *Dasyprocta*	(2.6 cm, 3.8 g)		53	NA	NA
Dasyprocta[3]	*Dipteryx panamensis* (5 - 6 cm, 18 - 26 g)		8	92	14 - 28
Dasyprocta[4] (78 % of seeds killed) and *Sciurus granatensis*	*Attalea butyracea* (ca. 3 cm)		7	93	43
Dasyproctidae[5]	*Carapa procera* (2 - 5.5 cm, 18 g)		37 - 84	16 - 63	28 - 45
Dasyprocta[6]	*Doliocarpus olivaceus* (1.1 cm, 0.21 g)		4	96	7
	Cupania latifolia (1.1 cm, 0.74 g)		0	100	1
	Eugenia coloradensis (1.3 cm, 1.3 g)		15	85	14
	Brosimum alicastrum (1.8 cm, 2.2 g)		33	67	29
	Virola nobilis (2 cm, 3 g)		74	26	18
	Licania platypus (2.4 cm, 6.3 g)		35	65	24
	Gustavia superba (1 - 3.5 cm, 13 g)		92	8	16 - 25
Heteromys[7]		Site			
Wet season 1996	*Astrocaryum mexicanum* (3 - 6 cm, 15 g)	A	7	0	93
		B	7	0	93
Wet season 1997	*Astrocaryum mexicanum*	A	15	85	55
		B	21	79	47
Dry season 1997	*Astrocaryum mexicanum*	A	5	95	30
		B	1.4	99	23
Dry season 1997	*Ampel. hottlei* (1.3 cm, ca. 1.5 g)	A	23	77	31
		B	16	84	36
Wet season 1997	*Pouteria sapota* (8 cm, 50 g)	A	0	18[†]	2[†]
		B	0	0	0
Dasyprocta	*Pouteria sapota*	A	15[‡]	67	0
		B	63[‡]	37	20

[†] % killed (eaten) from open plots only and % unknown from exclosures only;
[‡] %'s calculated from open plots only;
[1] see Forget 1990; [2] Forget 1991; [3] Forget 1993; [4] Forget et al. 1994; [5] Forget 1996; [6] Forget pers. comm. & Forget et al. 1998; [7] Brewer & Rejmánek (this study).

Burial of seeds to depths of greater than 20 cm inhibits seedling survival, and no seeds have survived from seeds planted at depths of 40 cm (n = 98) – the depth at which seeds have been taken into burrows (Brewer unpubl. data). *Ampelocera* seeds readily germinate on the soil surface (Brewer pers. obs.), and *Pouteria* seeds not removed by rodents germinated readily in the wet season (mean % germination = 68, SD = 21, range = 33 - 100, 10 plots).

Most seeds were found on the surface of the forest floor: in logs, hollow leaf sheaths of *Attalea cohune* (*Palmae*), under herbaceous cover, or next to tree buttresses.

Table 6. Mean time in days (± SD) that fruits/seeds, buried by mammals, remained in the soil or under litter. Retrieved seeds are those which were excavated by mammals. Unretrieved seeds remained buried at the end of the study.

Seed species	Retrieved seeds		Unretrieved seeds	
	Seeds (*n*)	Days	Seeds (*n*)	Days
Astrocaryum: 1996 wet season	5	3.8 ± 3.0	6	8-21+
Astrocaryum: 1997 dry season	3	25.0 ± 30.0	0	-
Astrocaryum: 1997 wet season	10	7.8 ± 12.6	4	75+
Pouteria	9	12.0 ± 4.6	4	45-79+
Ampelocera	23	11.0 ± 9.7	0	-

There were proportionally large numbers of tags found to be protruding from burrows in the forest floor (Figs. 1 and 3; entrances 2-6 cm in diameter; 40-50 cm vertical burrow depth). Only 13% of *Astrocaryum* fruits removed by mammals in the 1996 experiment, using the 60-cm tags, were found. Many more fruits were found in 1997, however, when 150 cm tags were used (Table 5).

Distances of removed seeds from the plots were almost always less than 15 m (Table 4), but two *Pouteria* seeds were found buried by agoutis at 34 and 93 m away. For all experiments, no significant difference in distance of seeds removed was found between open plots and exclosures ($p>0.05$, statistics not shown). No significant differences among experiments in distances of seeds moved on the surface ($p = 0.13$) or buried in the forest floor ($p = 0.10$) were found. Seeds of *Ampelocera*, and *Astrocaryum* fruits in the wet season, were taken into burrows significantly farther away than *Astrocaryum* fruits were in the dry season (Scheffe's test, $p = 0.001$). Seeds moved to burrows always ended up significantly farther away than seeds moved to the surface in all experiments except that using *Pouteria* seeds, which were never taken to burrows (Table 4).

Small mammal trapping

Trapping with *Astrocaryum* nuts resulted in high trap success at site A (mean = 30% per night; 54 individuals total) and relatively low success at site B (mean = 8% per night; 21 individuals total) for *Heteromys desmarestianus* (hereafter *Heteromys*). Percent of recaptures of *Heteromys* stabilized at about 80% per day. *Tylomys nudicaudus* was the only other known seed predator captured (one individual, one capture). Like *Heteromys*, the individual of *Tylomys* consumed some bait while trapped, but the other mammals trapped (*Didelphus virginiana Marmosa* cf. *mexicana*, one individual and one capture each) did not eat the bait and are not known to be granivores (e.g. Emmons & Feer 1997). The only granivore species caught on the forest floor in a prior trapping session, using traps baited with peanut butter and oats, was *Heteromys desmarestianus*.

Discussion

Seed dispersal and predation by small rodents

Heteromys desmarestianus is responsible for removal of most, if not all, of the *Astrocaryum* and *Ampelocera* fruits in the area. This rodent is the only representative of the genus in this part of Central America (Rogers & Schmidly 1982) and the only burrowing small rodent in the area (Emmons & Feer 1997). Observations and trapping results revealed that it is the most common small mammal, which is in agreement with data from an adjacent forest (Rabinowitz & Nottingham 1989). For *Astrocaryum* and *Ampelocera*, there were no significant differences in seed removal and fates from open and exclosed plots; hence large mammals were not important in the removal of these seeds. Our experiments and trapping results confirm the prediction (Martínez-Gallardo & Sánchez-Cordero 1993) that removal rate of *Astrocaryum* fruits by *Heteromys* should be high.

Seed removal, however, does not necessarily equal seed predation. Based on observations of captive individuals of *Heteromys* (Fleming & Brown 1975) and wild and captive *Proechimys* spp. (e.g. Forget 1991; Adler 1995; Hoch & Adler 1997), some researchers have predicted that small rodents may be significant dispersers (by burial) of seeds. Our results and observations clearly show that *Heteromys* in our study area bury a large percentage of seeds of two tree species, and they reveal the dispersal by burial (though not quantified) of at least four other tree seed species. Like agoutis (*Dasyprocta* spp.), acouchies (*Myoprocta* spp.) and spiny rats (*Proechimys semispinosus.*), *Heteromys* disperses most seeds ≤ 10 m away (Table 4). Unlike *Proechimys*, which seems to bury seeds under the leaf litter (Forget 1991), *Heteromys* buries seeds in the soil. Short-distance secondary dispersal will not move most seeds out of the influence of the parent tree where seed/seedling mortality may be higher (Janzen 1970; Connell 1971; Howe 1993). Buried seeds, however, stand a higher chance of escaping predation than seeds on the soil surface (Vander Wall 1993; Brewer & Rejmánek unpubl.), for it is less economical for competitors to pilfer scatterhoarded caches than to forage for food (Smith & Reichman 1984). For tree species that have survival and/or germination enhanced by burial, subtle differences in dispersal behavior by small rodents might result in different patterns of tree seedling recruitment between *Heteromys* and *Proechimys*-dominated forests.

Not all seeds handled by *Heteromys* will suffer high rates of predation or burial by these mice (Sánchez-Cordero & Martínez-Gallardo 1998). No significant difference was found in removal of the *Pouteria* seeds between open and exclosure plots, although a large

difference in *Pouteria* removal by small rodents was observed between the two sites (Fig. 2). *Pouteria* seeds taken from open plots were also more likely to be buried and/or eaten by large than small rodents. Perhaps because of their heavy weight, large size, and thick coats, *Pouteria* seeds may present more of a risk (handling unwieldy seeds might increase susceptibility to predators) and/or cost than benefit to small rodents except under conditions of very low food availability. That *Heteromys* is at all capable of moving and consuming the exceptionally large seeds of *Pouteria sapota* means that for all but a very few seed species, seed size does not necessarily limit foraging by *Heteromys*.

This study indicates that seed predation and dispersal by small rodents is likely a complex process, and therefore should impact tree recruitment in complex ways. Seed removal rates and fate differed dramatically by seed species, season (for *Astrocaryum*), year, site (*Astrocaryum* and *Pouteria*) (Figs. 2 and 3), and among replicates (CVs > 100% for removal rates were common) within sites. Moreover, these effects can interact. Removal rates of *Astrocaryum* fruits, for example, differed by site, but the direction and magnitude of the difference depended on season and year.

Trapping results for *Heteromys* in Belize (Disney 1968; Rabinowitz & Nottingham 1989), and for small rodents throughout the Neotropics (e.g. Gliwicz 1984; Adler & Beatty 1997; Sánchez-Cordero & Martínez-Gallardo 1998) demonstrate that small rodent abundances vary greatly by year, season, and on small spatial scales. Differences in small-rodent abundance have been shown to affect the relative amounts of seeds consumed in tropical wet forests (Hoch & Adler 1997), and variation in abundance of other *Heteromyid* species has been shown to be a major determinant of the plant abundance and composition in deserts (e.g. Brown et al. 1979). Fluctuations in small rodent abundance over time and space, and variation in foraging intensity and seed preferences over space could be a potent force in controlling variation in tree seed dispersal and survival and therefore spatial and temporal patterns of recruitment of tree species.

Finally, although the use of exclosures in removal experiments limits access to seeds to certain mammals, such experiments may be misleading without following seed fates. Removal rates of *Pouteria* seeds between exclosures and open plots were nearly identical for one site (Fig. 2). The fates of those seeds, however, revealed that removal was controlled by two different mammals (small rodents for exclosure seeds, agoutis for 80% of seeds in open plots). Seeds of *Ampelocera* and *Astrocaryum* were sometimes removed from open plots faster or slower than those seeds in exclosure plots (Fig. 2), even though the fates of the seeds clearly revealed that only small rodents were responsible for seed removal.

Broader ecological and conservation implications

The importance of caviomorph rodents as terrestrial seed dispersers has been emphasized in the literature. Leigh (1996), for example, pointed out that agoutis (*Dasyprocta* spp.), which bury seeds a few cm under the soil surface, "may turn out to be keystone animals for the preservation of tree diversity". Smythe (1989) suggested that agoutis are a vital link in the survival of a 'keystone' palm/plant resource (*Astrocaryum standleyanum*) and thus play a pivotal role in the survival of an entire forest. Yet small, not large rodents are more likely to be dominant terrestrial seed dispersers for at least two reasons.

First, dispersal of *Pouteria* and other very large seeds, and dispersal in habitats with unusually high densities of agoutis (e.g. Barro Colorado Island; Glanz 1990), likely represent exceptional cases of control over secondary seed dispersal by caviomorph rodents. Agoutis handle a variety of seed sizes, but caching rate of seeds by agoutis is much higher for large than small seeds (Hallwachs 1986; Forget et al. 1998). Large and very large seeds represent a small fraction of those tree seeds that may be found in a tropical wet forest. For example, analysing van Roosmalen's (1985) data, we found that only 2% of the 1446 tree species in French Guiana have seeds >4 cm in any one dimension and only 0.7% were >6cm in any dimension. Many large-seeded species may represent those tree species which are – through historical extinctions of large mammals – able to persist without their original primary dispersers, are 'anachronisms' (Janzen & Martin 1982), are dispersed by more than one animal species or means (e.g. water), and/or are maintained through human intervention (e.g. van Roosmalen 1985; Gómez-Pompa et al. 1987; Remmers & Koeijer 1992).

Second, the complete removal and destruction of most *Astrocaryum* and *Ampelocera* seeds from the surface of the forest floor at our sites is consistent with other studies which point to small rodents as important, even primary, granivores in Neotropical forests (e.g. Vandermeer et al. 1979; Coates-Estrada & Estrada 1988; Terborgh & Wright 1994; Forget 1991; Adler 1995; Asquith et al. 1997; Hoch & Adler 1997; Sánchez-Cordero & Martínez-Gallardo 1998). Spiny pocket mice (*Heteromys* and *Liomys*) and spiny rats (*Proechimys*) are the most ubiquitous (Emmons & Feer 1997) and are collectively the most abundant terrestrial mammals in most Neotropical forests (Eisenberg 1980; Robinson & Redford 1986). *Proechimys* spp. have the highest total (mammalian) energy intake per area of one forest where data exist (Janson & Emmons 1990), and *Heteromys* and *Proechimys* consume a wide variety of seeds (Martínez-Gallardo & Sánchez-Cordero 1993; Adler 1995). High densities, relatively high metabolic and reproductive rates, and morphological adaptations such

as strong jaws, and cheek pouches for carrying large quantities of food combine to make these rodents very efficient and effective granivores.

In the process of granivory, small tropical rodents disperse and bury a significant proportion of seeds (Table 5, Fig. 3). Like other mammals such as agoutis (Hallwachs 1986; Forget 1991), *Heteromys* retrieved ≥ 95% of buried seeds. Yet, some seeds dispersed by small rodents will escape predation by being forgotten or left by a disperser that dies or emigrates, or by germinating before the dipserser can recover the seed. Compounded over the reproductive lifetime of a tree and the thousands of seeds produced by each individual in a year, this very small percentage of forgotten seeds should grow into an important amount of seedling recruitment.

It seems doubtful that there exist keystone seed predators/dispersers in systems of such complexity as those found in tropical wet forests. The loss of large mammalian seed dispersers/predators through hunting does not mean that most trees will be without terrestrial seed dispersers. Nevertheless, identification of tree species that are extinction prone under heavy hunting scenarios, and predicting changes in forest structure as faunas change, should have high research priority. Studies of seed removal in the tropics must identify and quantify seed fates in order to provide meaningful insights into the effects of mammals on the dynamics and patterns of tree recruitment in forests.

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