

Multi-species fruit and seed removal in a tropical deciduous forest in Mexico

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Abstract: We determined patterns of post-dispersal fruit and seed removal for 11 common native plants, as well as sunflower seeds (*Helianthus annuus* L.), within a tropical deciduous forest in Jalisco, Mexico. Removal values were high in *Delonix regia* (Bojer) Raf. (90%), *Crescentia alata* Kunth. (87%), *H. annuus* (81%), *Pithecellobium dulce* (Roxb.) Benth (81%), *Albizia occidentalis* Brandegees (80%), *Coccoloba barbadensis* Jacq. (80%), *Recchia mexicana* DC. (80%), *Caesalpinia pulcherrima* (L.) Sw. (79%), *Enterolobium cyclocarpum* (Jacq.) Griseb. (73%), moderate in *Guazuma ulmifolia* Lam. (42%) and *Celtis iguanaeus* Sarg. (44%), and low in *Amphipterygium adstringens* (Schlechtend.) Schiede ex Standl. (17%). Low removal rates (29%) in experimental patches open only to arthropods suggest that arthropods have a minor role in removing fruits and seeds of these species. Removal values were high in experimental patches open to all potential agents (77%) and semipermeable patches open to forest-dwelling rodents (76%), suggesting that the latter group, the most abundant terrestrial mammal in this forest, was an important agent for removing the fruits and seeds of study plants. Removal values were higher in experimental patches located in tropical deciduous forest than in tropical semideciduous forest, as well as higher in high density (patches of 30 fruits or seeds) than in low density (patches of five fruits or seeds) experimental patches for most study plants. Mice appear to selectively remove and hoard fruits and seeds according to their energy and nutritional content and the presence of secondary metabolites, and from high-density food patches and preferred habitats. Nonindependent effects of species, habitat, and density suggest that a complex interplay of factors determines fruit and seed removal for the plants examined from the Chamela tropical forest.

Key words: fruits, forest-dwelling rodents, Mexico, post-dispersal removal, seeds, tropical deciduous forest.

Résumé : Les auteurs ont déterminé les patrons de prélèvement post-dispersion des fruits et des graines, chez 11 plantes indigènes communes, ainsi que des graines du tournesol (*Helianthus annuus* L.), dans une forêt tropicale décidue à Jalisco, au Mexique. Les valeurs de prélèvement étaient élevées chez le *Delonix regia* (Bojer) Raf. (90 %), le *Crescentia alata* Kunth. (87 %), l' *H. annuus* (81 %), le *Pithecellobium dulce* (Roxb.) Benth (81 %), l' *Albizia occidentalis* Brandegees (80%), le *Coccoloba barbadensis* Jacq. (80 %), le *Recchia mexicana* DC. (80 %), le *Caesalpinia pulcherrima* (L.) Sw. (79 %), l' *Enterolobium cyclocarpum* (Jacq.) Griseb. (73 %), modérées chez le *Guazuma ulmifolia* Lam. (42 %) et le *Celtis iguanaeus* Sarg. (44 %) et faible chez l' *Amphipterygium adstringens* (Schlechtend.) Schiede ex Standl. (17 %). Les faibles taux de prélèvement (29 %) dans des plages ouvertes seulement aux arthropodes suggèrent que leur rôle est modeste dans le prélèvement des fruits et des graines, chez ces espèces. Les valeurs de prélèvement étaient élevées dans les plages expérimentales ouvertes à tous les agents potentiels (77 %) et les plages semi-perméables aux rongeurs forestiers (76 %), ce qui suggère que ce dernier groupe, constituant les mammifères les plus abondants de cette forêt, seraient des agents de prélèvement importants de fruits et de graines chez les espèces étudiées. Les valeurs de prélèvement étaient élevées dans les plages expérimentales situées dans la forêt tropicale décidue comparativement à la forêt semi-décidue, aussi bien que de forte densité (plages avec 30 fruits ou graines) vs faible densité (plages avec cinq fruits ou graines), chez la majorité des espèces étudiées. Les souris semblent prélever sélectivement et accumuler les fruits et les graines selon leur teneur énergétique et nutritionnelle et la présence de métabolites secondaires, la forte densité des plages en nutriments et à partir d'habitat préférés. Les effets d'indépendance par rapport à l'espèce, l'habitat et la densité suggèrent une interaction complexe de facteurs qui déterminent le prélèvement des fruits et des graines, chez les plantes examinées de la forêt tropicale de Chamela.

Mots clés : fruits, rongeurs forestiers, Mexique, prélèvement post-dispersion, graines, forêt tropicale décidue.

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Introduction

Tropical forests demonstrate an exceptionally rich biological diversity and complex plant–animal interactions (Howe and Smallwood 1982; Estrada and Fleming 1986; Forget et al. 1998, 2005). Diversity of seed-producing plants and seed consumers leads to nonrandom patterns of fruit and seed removal that are still poorly understood (Whelan et al. 1991; Schupp 1998*a*, 1998*b*; Gilbert et al. 2001). Previous studies have shown that fruits and seeds falling below parent trees have little chance of establishing as reproductive individuals; plants thus need animals to remove fruits and seeds from the parent tree to increase seedling survival (Janzen 1969, 1971, 1983, 1986; Terborgh 1986). Alternatively, some plants produce massive seed crops to satiate predators and insure that some seeds survive to germination (Janzen 1971, 1986). The fate of fruits and seeds depends largely on the feeding behaviour of animals, as consumers can act as seed predators and (or) dispersal agents (Estrada and Fleming 1986; Smythe 1986; Forget et al. 1998, 2005). Post-dispersal fruit and seed removal by animals can significantly affect seedling recruitment, thus shaping the diversity, distribution, and structure of plant communities (Forget et al. 1998; Connell and Green 2001). Previous studies have mainly focused on patterns of fruit or seed removal for individual plant species (Sork 1987; Forget 1993, 1996; Forget et al. 1994, 1998; Schupp 1998*a*, 1998*b*). A community-level approach of post-dispersal fruit and seed removal may enhance our understanding of the underlying causes of observed nonrandom patterns in seedling survival (DeSteven 1994; Harms et al. 2000; Nathan and Muller-Landau 2000; Gilbert et al. 2001; Andrew et al. 2003).

Terrestrial mammals are known to selectively remove and consume large amounts of the fruits and seeds that fall to the forest floor in the Neotropics (Janzen 1971, 1983, 1986; Howe and Smallwood 1982; Estrada and Fleming 1986; Smythe 1986; Schupp 1998*a*, 1998*b*). Several studies have documented that the type of fruit and seed, fruit and seed patch density, and the habitat where the fruits and seeds fall can influence post-dispersal removal (Wilson and Whelan 1990; Whelan et al. 1991). Fruits and seeds containing high nutritional and (or) energy values are preferred, while those with high doses of toxic metabolites are ignored (Janzen 1969, 1971, 1981). Terrestrial mammals may selectively forage in dense patches of fruits and seeds to maximize energy intake (Wilson and Whelan 1990; Nathan and Muller-Landau 2000). Location or habitat where fruits and seeds fall to the forest floor can also determine removal rates (Hay and Fuller 1981; Manson and Stiles 1998). For example, several forest-dwelling mammals, such as species of the spiny pocket mice genera *Liomys* and *Heteromys*, select forest habitats according to predation risks, food availability, and (or) facilities for building nesting sites (Janzen 1982*a*, 1982*b*, 1983, 1986; Sánchez-Cordero and Martínez-Galardo 1998; Brewer and Rejmanek 1999; Nathan and Muller-Landau 2000; Sánchez-Rojas et al. 2004).

Previously, we conducted laboratory and field experiments with four common plant species and found that species, seed density, seed quality, and microhabitat differentially affected post-dispersal fruit and seed removal in a tropical deciduous forest in Mexico (Briones and

Sánchez-Cordero 1999; Sánchez-Rojas et al. 2004). Factors influencing fruit and seed removal correlated with the foraging behavior of the heteromyid *Liomys pictus*, the most abundant forest-dwelling rodent in this forest (Sánchez-Cordero and Fleming 1993); *L. pictus* removed more highly nutritious seeds from high-density food patches than from low-density food patches and from preferred microhabitats than from poor microhabitats; they also disregarded seeds with little nutritional value and (or) seeds containing secondary metabolites (Briones and Sánchez-Cordero 1999; Sánchez-Rojas et al. 2004).

Here, we expand these studies adding 11 common native plant species that produce massive crops and that were collected from spiny pocket mice cheek-pouches, as well as sunflower seeds (for a total of 12 species); the experiments were repeated in the same study site. This community-level approach provides more robust information on nonrandom patterns of seedling recruitment based on the feeding preferences of removal agents on this forest (Beckage and Clark 2005). Previously, we determined the nutritional value (percent organic matter, percent fiber, percent protein, and percent lipids) and chemical composition (presence of alkaloids, flavonoids, terpenes, and glucosides) of the fruits and seeds of the study species and determined their dietary value to spiny pocket mice based on monospecific diets in laboratory experiments (Table 1) (Briones and Sánchez-Cordero 1999). Our first objective was to test the hypothesis that highly nutritious fruits and seeds are selectively removed compared with fruits and seeds with low nutritional value and (or) fruits and seed containing toxic metabolites. Specifically, we predicted high removal rates for fruits and seeds with high dietary values (i.e., caged spiny pocket mice maintained or increased weight when on the corresponding monospecific diet) and low removal rates for fruits and seeds with low dietary values (i.e., caged spiny pocket mice lost weight when on the corresponding monospecific diet) (Briones and Sánchez-Cordero 1999). We further determined (1) the importance of forest-dwelling rodents in comparison with other vertebrates and arthropods in removing these fruits and seeds from the forest floor, and (2) if fruit and seed removal was habitat dependent and (or) density dependent.

Materials and methods

Study site

This study was conducted at the Chamela Biological Station located in Jalisco, Mexico (<http://www.ibiologia.unam.mx/chamela>). The study site occupies 1600 ha and is dominated by lowland tropical deciduous forest together with widespread riparian corridors of tropical semideciduous forests (Lott et al. 1987). Elevation ranges from 150 to 530 m. The mean annual temperature is 25 °C (ranging from 15 to 32 °C). Mean annual precipitation is 748 mm (ranging from 584 to 1393 mm), with most precipitation occurring from July through October; the dry season extends from February to May with less than 50 mm per month (Bullock 1986).

Plant species

We selected fruits and seeds from 11 native common plants that produce large crops and that are found at the

Table 1. Natural history of the study plants from the Chamela tropical deciduous forest in Jalisco, México (Lott et al. 1987).

Species	Life form	Fruit fall	Seed size (cm) ^a	Seeds per matter (%)	Organic (%)	Fiber (%)	Protein (%) ^b	Lipid ^b	Secondary metabolites ^c		
									Alkaloids	Flavonoids	Glucosides
Bignoniaceae											
<i>Crescentia alata</i>	Tree	October	0.6–1.0	200–800	96.06a	57.31a	1.10bc	31.22a	Low +	+	High +
Julianaceae											
<i>Amphipterygium adstringen</i>	Tree	October	1.0–2.0	1	95.95a	70.37a	0.96c	1.46b	Low +	Low +	–
Leguminosae											
<i>Albizia occidentalis</i>	Tree	October	0.5–0.9	6–18	95.75a	25.82b	4.62b	0.11c	–	–	+
<i>Caesalpinia pulcherrima</i>	Tree	November	0.7–1.0	2–8	97.49a	11.87c	2.56b	4.21b	Low +	Low +	+
<i>Delonix regia</i>	Tree	June	1.5–1.8	8–16	95.92a	24.34b	2.34b	1.73bc	–	–	High +
<i>Enterolobium cyclocarpum</i>	Tree	June	1.4–2.1	6–18	95.05a	14.32c	1.77bc	0.71c	–	+	High +
<i>Pithecellobium dulce</i>	Tree	November– December	0.8–11.0	6–12	96.78a	49.50ab	0.70 c	13.53b	Low +	–	+
Ulmaceae											
<i>Celtis iguanaeus</i>	Shrub	November	0.4–0.6	1	81.92b	8.54c	3.17b	1.97b	–	Low +	High +
Polygonaceae											
<i>Coccoloba barbadensis</i>	Tree	December	0.3–0.6	1	96.16a	21.23b	0.99c	1.15b	Low +	Low +	High +
Sterculiaceae											
<i>Guazuma ulmifolia</i>	Tree	March	0.2–0.3	50–100	96.30a	44.67ab	0.72c	1.09bc	Low +	–	Low +
Simaroubaceae											
<i>Recchia mexicana</i>	Tree	April	0.9–1.6	1	97.93a	55.60a	0.42c	6.98b	Low +	–	Low +
Compositae											
<i>Helianthus annuus</i>	Plant	—	—	—	95.39a	47.57ab	24.80a	43.18a	–	–	–

Note: Fruits and seeds (or parts of them) were identified from the cheekpouches of wild-caught spiny pocket mice (*Liomys pictus*). Fruit and seed organic matter (total dry mass – mass of ash), nutritional content, and secondary metabolites (methanol extracts) of the study plants, as well as their dietary value to spiny pocket mice, were determined in previous studies (Briones and Sánchez-Cordero 1999; Sánchez-Rojas et al. 2004). None of the study plants contained terpen extracts (for complete details, see Briones and Sánchez-Cordero 1999). For the chemical analyses, values followed by the same letter are not statistically different according to a least-significant-difference LSD test ($P < 0.05$).

^aRanges are for a sample of 100 seeds of each study plant.

^bCrude amount per 100 g of fruit or seed.

^cSecondary metabolites were ranked as high positive (high +), positive (+), low positive (low +), or absent (–), according to methanol extract concentrations (taken from Briones and Sánchez-Cordero 1999).

study site. Details of their basic natural history, fruit and seed size, fruiting season, and nutritional and chemical composition are provided elsewhere (see Table 1; Briones and Sánchez-Cordero 1999; Noguera et al. 2002). Fruits or seeds were collected from the forest floor during fruit fall peaks, but experiments were conducted after the fruiting season of the study plants after animals had removed most food items from the forest floor; we intended to control for the effects of background food availability and solely quantify the removal response of removal agents for the study species.

The species used and the dates of removal experiments were as follows: fruits of the tree *Amphipterygium adstringens* (Schlechtend.) Schiede ex Standl. (Julianaceae) in November 1992, the shrub *Celtis iguanaeus* Sarg. (Ulmaceae) in February 1993, the tree *Coccoloba barbadensis* Jacq. (Polygonaceae) in May 1993, and the tree *Guazuma ulmifolia* Lam. (Sterculiaceae) in June 1993; seeds of the trees *Albizia occidentalis* Brandege (Leguminosae) in January 1993, *Caesalpinia pulcherrima* (L.) Sw. (Leguminosae) in June 1992, *Delonix regia* (Bojer) Raf. (Leguminosae) in July 1992, *Enterolobium cyclocarpum* (Jacq.) Griseb. (Leguminosae) in September 1992, *Pithecellobium dulce* (Roxb.) Benth (Leguminosae) in April 1993, *Crescentia alata* Kunth. (Bignoniaceae) in August 1992, and *Recchia mexicana* DC. (Simaroubaceae) in July 1992. Sunflower (*Helianthus annuus* L. (Compositae)) seeds were included for comparison in the experiments in December 1992.

Experimental fruit and seed patches

Fruits or seeds of individual species were placed on squares (25 cm × 25 cm) of ground cleared of litter as the experimental food patches. Fruits and seeds removed from each experimental patch were recorded daily at 0600 for five consecutive days.

We used a total of six randomly placed grids (1-ha each) in fruit and seed habitat-dependent and density-dependent removal experiments: three grids were located in tropical deciduous forest habitat and three grids in tropical semideciduous forest habitat. Three treatments were applied: enclosures, semipermeable enclosures, and controls. The enclosures were experimental patches enclosed with 1.5 cm mesh wire cages that restricted access to only arthropods. The semipermeable enclosures were experimental patches enclosed with mesh wire cages that each had a 3 cm opening providing access to arthropods and forest-dwelling rodents only, and controls, experimental patches allowing access to all potential removal agents (see Sánchez-Cordero and Martínez-Gallardo 1998).

Within each grid, we randomly placed (*i*) six food patches each containing 30 fruits or seeds (high-density patches) and consisting of three enclosure replicates, three semipermeable enclosure replicates, and three control replicates (54 experimental patches in total); and (*ii*) six food patches each containing 5 fruits or seeds (low-density patches) and consisting of three semipermeable enclosure replicates and three control replicates (36 experimental patches in total). We did not include enclosure patches within the low density patches because of technical difficulties collecting enough fruits or seeds. The fruit and seed densities were selected based on recommendations by Sánchez-Cordero and Martínez-Gallardo (1998) and Sánchez-Rojas et al. (2004) given that densities

“naturally” occurring in the forest floor are not known for the study plants. A total of 90 experimental patches including a total of 2160 fruits or seeds were used for each study plant.

We randomly placed 40 sand beds (30 cm × 30 cm) beside the experimental patches for tracking potential agents (mainly terrestrial mammals, birds, and arthropods) removing fruits or seeds during the 5 d experiments for each study plant. Tracks and trails observed for each sand bed during the removal experiments were counted as a record.

Statistical analyses

The percentage of fruits or seeds removed after the 5 d experiments were arcsine-transformed for statistical analyses. Bartlett's test was not significant, indicating homogeneity of variances ($P = 0.90\text{--}0.96$; Zar 1999). We conducted 1-way ANOVAs to test for the overall effect of species and treatment. A four-way ANOVA was conducted to test for the effects of species (12 study plants), habitat (two levels, i.e., tropical deciduous forest and tropical semi-deciduous forest), density (two levels, i.e., low and high), and treatment (two levels, i.e., semipermeable enclosure and non-enclosure; see below) on post-dispersal fruit and seed removal of individual species.

Results

We observed significant differences in post-dispersal removal rates between plant species ($F = 40.17$, $df = 11$, $P < 0.0001$), ranging from high values in *D. regia* (90%), *Crescentia alata* (87%), *H. annuus* (81%), *P. dulces* (81%), *Albizia occidentalis* (80%), *Coccoloba barbadensis* (80%), *R. mexicana* (80%), *Caesalpinia pulcherrima* (79%), and *E. cyclocarpum* (73%), moderate values for *Celtis iguanaeus* (44%) and *G. ulmifolia* (42%), and low values for *Amphipterygium adstringens* (17%) (Table 2). There were significant differences in fruit and seed removal between treatments ($F_{[27,73]} = 107.21$, $P < 0.0001$). Full enclosure treatments had removal values below 35% for all study plants, except for *Crescentia alata*, which reached 75%, and were excluded from further analyses.

Significant differences in post-dispersal removal rates were observed between experimental fruit and seed patches located in tropical deciduous forest and those located in tropical semideciduous forest for most study plants (Table 1). *Guazuma ulmifolia ulmifolia*, *Albizia occidentalis*, *R. mexicana*, *Caesalpinia pulcherrima*, *H. annuus*, *P. dulces*, *E. cyclocarpum*, and *Celtis iguanaeus* had higher removal rates in tropical deciduous forest. *Crescentia alata*, *Amphipterygium adstringens*, and *Coccoloba barbadensis* had higher removal rates in tropical semideciduous forest. *D. regia* showed similar removal values in both habitats. We observed a significant species × habitat interaction (Table 2).

More fruit and seeds were removed from high-density food patches than from low-density food patches in most study plants (Table 3); *D. regia*, *Crescentia alata*, and *Albizia occidentalis* had similar removal values between density patches (Fig. 1). We observed significant species × density, habitat × density, and species × habitat × density interactions (Table 3).

Table 2. Influence of forest type (tropical deciduous forest and tropical semi-deciduous forest) and treatment on fruit and seed removal in 90 experimental food patches of 11 native plants and sunflowers (*Helianthus annuus*) from the forest floor at the Chamela Biological Station, Jalisco, Mexico.

	Tropical deciduous forest			Tropical semideciduous forest		
	Exclosure	Semipermeable enclosure	Control	Exclosure	Semipermeable enclosure	Control
<i>Caesalpinia pulcherrima</i>	16.1±13.9	90.0	72.4±19.3	16.1±13.9	63.4±4.7	80.1±15.7
<i>Delonyx regia</i>	8.0±13.9	90.0	90.0	8.4±13.9	90.0	90.0
<i>Crescentia alata</i>	53.3±37.5	90.0	90.0	78.5±20.4	90.0	90.0
<i>Enterolobium cyclocarpum</i>	30.0±51.9	90.0	90.0	13.1±22.7	79.3±21.7	84.8±12.7
<i>Amphipterygium adstringens</i>	0	12.2±9.9	14.4±8.6	10.4±17.9	35.6±14.7	33.2±10.1
<i>Helianthus annuus</i>	0	75.0±24.0	90.0	3.5±6.0	90.0	90.0
<i>Albizia occidentalis</i>	24.5±23.5	46.4±9.4	56.2±19.2	3.5±6.0	46.7±24.3	50.9±13.9
<i>Celtis iguanaeus</i>	30.0±51.9	90.0	90.0	30.0±51.9	79.0±17.1	78.4±18.0
<i>Pithecellobium dulce</i>	0	89.2±1.9	90.0	0	84.1±14.4	90.0
<i>Coccoloba barbadensis</i>	13.3±11.6	75.1±33.2	90.0	10.7±12.3	90.0	84.8±12.7
<i>Guazuma ulmifolia</i>	6.9±6.0	38.0±11.7	44.3±30.2	3.5±6.0	53.8±10.6	75.5±15.8
<i>Recchia mexicana</i>	17.5±15.9	74.9±5.9	85.0±7.8	19.8±18.0	85.9±6.5	83.3±7.3

Note: Three treatments were applied: exclosures, experimental patches where only arthropods had access; semipermeable exclosures, where only arthropods and forest-dwelling rodents had access; and controls, where all potential removal agents had access. Seeds and fruits were removed after 5 d. Means and standard deviations of arcsine-transformed percentage removal values are shown. See Materials and methods for details of the experimental protocols.

There were no significant differences in seed and fruit removal rates between semipermeable enclosure and control treatments, although we observed significant species × treatment, species × habitat × treatment, species × density × treatment, species × habitat × density × treatment interactions. No other interactions between factors were observed (Table 3). Lastly, more than 75% of sand beds recorded only tracks of forest-dwelling rodents, particularly spiny pocket mice, on the experimental food patches for most study plants; the only exception was in the *Amphipterygium adstringens* experiments, in which only 40% of sand beds recorded tracks in tropical semideciduous forest (Table 4).

Discussion

Post-dispersal removal agents

Similar post-dispersal removal rates for the semipermeable enclosure and control treatments suggests that forest-dwelling rodents were the main agents removing fruits and seeds of the study plants at the Chamela tropical forest. Frequent tracks on the sand beds indicated that spiny pocket mice (*L. pictus*) had an active foraging behavior; low records of tracks were observed only in *Amphipterygium adstringens* experiments, which had the lowest removal rates (Tables 2 and 4; Sánchez-Rojas et al. 2004). We found more trail records of arthropods, presumably ants, in experiments with *Crescentia alata*, *Caesalpinia pulcherrima*, and *R. mexicana* (Table 4). We found no solid evidence that other vertebrates, such as birds and reptiles, foraged on the experimental food patches; none of their tracks were recorded on the sand beds in our short-term experiments. Mice removed fruits and seeds from patches open to all potential removal agents (other vertebrates and arthropods) and from semipermeable patches to which only mice and arthropods had access. Low removal, except in *Crescentia alata*, from patches restricted to only arthropods suggests low preferences for these fruits and seeds and (or) a slower response

to detect them provided by our short-term experiments. In any case, other vertebrates and arthropods appeared to play a minor role in the immediate removal of study fruits and seeds from the Chamela tropical forest floor.

Previous studies have shown that the spiny pocket mouse, *L. pictus*, is the most abundant forest-dwelling mammal at Chamela, comprising more than 80% of total captures in nearly 10 000 trap/nights, and it has a spatial preference for tropical deciduous over tropical semideciduous forest at Chamela (Ceballos 1989; Sánchez-Cordero and Fleming 1993; Briones 1996; Sánchez-Rojas et al. 2004). Population size ranged from 5 to 45 individuals per ha, reaching the highest densities reported for spiny pocket mice (*Liomys*) in tropical deciduous forests (Sánchez-Cordero and Fleming 1993). Thus, post-dispersal fruit and seed removal of study plants species appeared to be substantially determined by foraging and space use decisions of spiny pocket mice, *L. pictus*.

Patterns of fruit and seed removal

Most study plant species had high removal rates, reaching values above 70%; only *Amphipterygium adstringens* had removal rates below 20%. In a previous study, we determined dietary values of the fruits and seeds of the study plants for spiny pocket mice under laboratory monospecific feeding trials. Based on fruit and seed energy content, nutritional value, and presence of secondary metabolites, we predicted field removal rates by spiny pocket mice (Briones and Sánchez-Cordero 1999) (Table 1). Energetically, *H. annuus*, *E. cyclocarpum*, *Albizia occidentalis*, *D. regia*, and *Coccoloba barbadensis* had high dietary values for spiny pocket mice, thus predicting high field removal rates. Conversely, *R. mexicana*, *Crescentia alata*, *G. ulmifolia*, *P. dulces*, *Caesalpinia pulcherrima*, *Amphipterygium adstringens*, and *Celtis iguanaeus* had low dietary values for spiny pocket mice, thus predicting low field removal rates (Briones and Sánchez-Cordero 1999) (Table 1). The high field removal

Table 3. Four-way ANOVA comparing fruits and seeds removed from experimental food patches, and depicting the effects of plant species (11 native plants and sunflower seeds), habitat (tropical deciduous and tropical semideciduous forest), and density (low; 5 fruits or seeds, and high; 30 fruits or seeds).

Source term	df	Sum of squares	Mean square	F ratio	P
Species	11	143464.1	13042.2	94.1	<0.0001
Habitat	1	871.5313	871.5	6.3	<0.01
Species × habitat	11	4807.927	437.1	3.2	<0.0005
Density	1	849882.1	849882.1	6128.9	<0.0001
Species × density	11	105081.3	9552.8	68.9	<0.0001
Habitat × density	1	712.5	712.5	5.1	<0.01
Species × habitat × density	11	3417.1	310.6	2.2	<0.01
Treatment	1	452.5	452.5	3.3	NS
Species × treatment	11	2901.8	263.8	1.9	<0.05
Habitat × treatment	1	232.9	232.9	1.7	NS
Species × habitat × treatment	1	4081.4	371.0	2.7	<0.005
Density × treatment	1	282.0	282.0	2.0	NS
Species × density × treatment	11	3090.8	280.9	2.0	<0.05
Habitat × density × treatment	1	362.3	362.3	2.6	NS
Species × habitat × density × treatment	11	3840.9	349.2	12.5	<0.01
Residual	192	26624.0	138.7		
Total (adjusted)	287	1150105.0			
Total	288				

Note: See Materials and methods for details of the experimental protocols.

rates observed for *D. regia*, *H. annuus*, *Coccoloba barbadosensis*, *Albizia occidentalis*, *E. cyclocarpum*, compared with moderate field removal rates for *G. ulmifolia* and *Celtis iguanaeus*, and low removal rates for *Amphipterygium adstringens* support the hypothesis that fruits and seeds of these plants were removed based on their energy content; in fact, spiny pocket mice, *L. pictus*, rapidly responded when encountering profitable alien seeds by removing virtually all sunflower seeds (rich in energy, protein, and lipid) in our short-term experiments (Table 2; Fig. 1; Briones and Sánchez-Cordero 1999; Sánchez-Rojas et al. 2004).

Crescentia alata, *P. dulces*, *R. mexicana*, and *Caesalpinia pulcherrima* also had high removal rates despite their low energy content, counter to our expectations (Tables 1 and 2; Briones and Sánchez-Cordero 1999). However, these plant species ranked highest in lipid content among the study plants (except for sunflower seeds), suggesting that spiny pocket mice also chose other nutritional and essential compounds when encountering fruits and seeds on the forest floor (Briones and Sánchez-Cordero 1999; Sánchez-Rojas et al. 2004). *Amphipterygium adstringens* had the lowest field removal values, likely because of its low energy, protein, and lipid contents (Table 1) (Briones and Sánchez-Cordero 1999). Further, most study fruits and seeds contained alkaloids, flavonoids, and (or) glucosides, suggesting that spiny pocket mice learn to avoid toxic metabolites in food items. Spiny pocket mice are capable of selectively avoiding even parts of fruits and seeds, presumably because they contain toxic metabolites. In experimental feeding trials, spiny pocket mice consumed only embryos, seeds, or pulps of the study plants (Briones and Sánchez-Cordero 1999). These results agree with previous findings where seeds containing toxic metabolites content were not removed, for example, the seeds of *Lonchocarpus eriocarinalis* and *Caesalpinia coriaria* (Leguminosae) at the same study site (Sánchez-

Rojas et al. 2004). In a Costa Rican tropical deciduous forest, spiny pocket mice, *Liomys salvini*, demonstrated similar feeding avoidance by rejecting seeds of various species of *Lonchocarpus* (Leguminosae), seeds known to contain toxic metabolites such as flavonoids (Janzen 1986). Additionally, other less abundant forest-dwelling rodents, such as the Marsh mouse (*Peromyscus perfulvus*) and the Michoacan deer mouse (*Osgoodomys banderanus*), with different food preferences, could have removed such low dietary fruits and seeds, influencing our interpretation.

Nonrandom field removal patterns for study plants suggests rapid learning to discern profitable fruits and seeds from the vast floristic diversity encountered in the Chamela forest floor. Spiny pocket mice store foraged food in burrows and then make dietary food choices to acquire energy and (or) essential elements and nutrients from specific parts of fruits or seeds (Briones and Sánchez-Cordero 1999; Sánchez-Rojas et al. 2004). Given that spiny pocket mice hoard predominantly foraged food items in their burrows (Janzen 1982a, 1982b, 1986; Sánchez-Cordero and Fleming 1993), it is likely that they acted mostly as seed predators on these study plants. We observed study fruits and seeds (or parts of them) in spiny pocket mice cheek-pouches and burrows, where food items are usually stored 20 cm below the forest floor (Briones and Sánchez-Cordero 1999; Sánchez-Rojas et al. 2004; personal observation), making successful germination highly unlikely. If spiny pocket mice and other animals eventually scatter-hoarded some study food items (Janzen 1986; Sánchez-Cordero and Fleming 1993), chances of successful germination will increase, although this secondary dispersal needs further investigation (Vander Wall et al. 2005). Our study, however, was not designed for determining fate of seeds, so we were unable to observe how frequently spiny pocket mice burrowed or scatter-hoarded the fruits and seeds included in our experiments.

Fig. 1. Effect of food patch density on post-dispersal removal of the fruits and seeds of the study plants in the Chamela Biological Station in western Mexico. Low-density food patches (white bars) included 5 fruits or seeds per patch and high-density food patches (black bars) included 30 fruits or seeds per patch. Removal values for only the semipermeable and nonenclosure treatments are included because because the enclosure treatments resulted in marginal values for most plants. C.p., *Caesalpinia pulcherrima*; D.r., *Delonyx regia*; C.a., *Crescentia alata*; C.i., *Celtis iguanaeus*; E.c., *Enterolobium cyclocarpum*; A.a., *Amphipterygium adstringens*; A.o., *Albizia occidentalis*; H.a., *Helianthus annuus*; P.d. *Pithecellobium dulces*; C.b., *Coccoloba barbadensis*; G.u., *Guazuma ulmifolia*; R.m., *Recchia mexicana*. See Materials and methods for details of the field experiments.

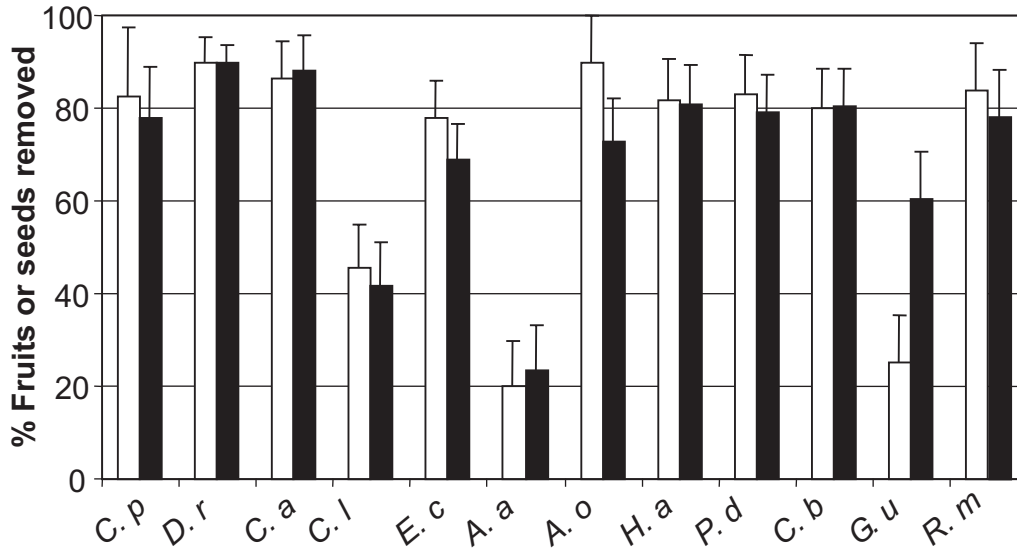


Table 4. Percentage of tracks and trails from potential removal agents recorded on 40 sand beds (30 cm × 30 cm) placed beside the experimental patches during five consecutive nights (total = 60 nights) for each study plant species.

	Tropical deciduous forest		Tropical semideciduous forest	
	Rodents*	Arthropods†	Rodents*	Arthropods†
<i>Caesalpinia pulcherrima</i>	85.0	15.0	80.0	20.0
<i>Delonyx regia</i>	100.0	0	95.0	5.0
<i>Crescentia alata</i>	80.0	20.0	75.0	25.0
<i>Enterolobium cyclocarpum</i>	95.0	0	90.0	5.0
<i>Amphipterygium adstringens</i>	50.0	0	40.0	5.0
<i>Helianthus annuus</i>	95.0	5.0	90.0	8.0
<i>Albizia occidentalis</i>	80.0	5.0	80.0	5.0
<i>Celtis iguanaeus</i>	90.0	5.0	80.0	5.0
<i>Pithecellobium dulces</i>	95.0	5.0	95.0	5.0
<i>Coccoloba barbadensis</i>	80.0	5.0	85.0	0
<i>Guazuma ulmifolia</i>	75.0	5.0	75.0	0
<i>Recchia mexicana</i>	80.0	10.0	75.0	10.0

Note: No obvious tracks from terrestrial vertebrates, such as birds or reptiles, were recorded in our short-term experiments. See Materials and methods for details of the experimental protocols.

*Track records of forest-dwelling rodents, mostly from spiny pocket mice (*Liomys pictus*).

†Trail records of arthropods, presumably ants.

Habitat-dependent fruit and seed removal

We observed significant differences in short-term field removal experiments between habitats (tropical deciduous forest vs. tropical semideciduous forest) for the study plants. Seeds of eight study plants were removed more often from tropical deciduous forest while seeds from three study plants were removed more often from the tropical semideciduous forest; *D. regia* was equally removed from both habitats (Table 2). This general pattern of habitat effect on seed removal agrees with a previous finding, where seeds of *H. annuus* and fruits of *Spondia purpurea* (Anacardiaceae)

were removed more frequently from tropical deciduous forest than from tropical semideciduous forest (Sánchez-Rojas et al. 2004), suggesting that spiny pocket mice have a habitat preference for actively forage such food items; a higher spiny pocket mouse density in tropical deciduous forests may have also contributed to more seeds and fruits being removed from this habitat (Sánchez-Cordero and Fleming 1993; Briones 1996).

Conversely, seeds with low removal rates such as those of *Amphipterygium adstringens* or seeds with low energy content such as those of *Crescentia alata* and *Coccoloba barba-*

densis (Briones and Sánchez-Cordero 1999) were removed more often from semideciduous forests than from tropical semideciduous forests (Table 2); this suggests that spiny pocket mice forage in tropical semideciduous forests once high rewarding fruits and seed resources have been depleted from the tropical deciduous forest. Alternatively, but not mutually exclusive, less active foraging in tropical semideciduous forests can be attributed to a higher predation risk. For example, ocelots (*Leopardus pardalis*) actively prey on spiny pocket mice and are commonly found in the tropical semideciduous forest at Chamela (De Villa et al. 2002). Habitat-dependent fruit and seed removal has been positively correlated with (or lack of) habitat preferences by forest-dwelling rodents in other tropical regions (Janzen 1986; Forget 1993, 1996, 2005; Sánchez-Cordero and Martínez-Gallardo 1998; Schupp 1988a, 1988b). These results may have important consequences for seedling recruitment for these plants in both habitats given that most study plants suffered high rates of fruit and seed removal at both site locations. Chamela tropical dry forest holds a high diversity of tree species (approximately 86 species/0.1 ha) but a low species density (Lott et al. 1987). Low tree species densities may partially result from a complex interplay of abiotic and biotic factors (such as seed predation) that prevents germination in most seeds produced by these study plants. Unfortunately, sufficient abundance data for most study plants to correlate habitat-related plant abundances with habitat-related seed removal does not exist (Lott et al. 1987; Lott and Atkinson 2002).

Density-dependent fruit and seed removal

Fruits and seeds were removed more often from high-density food patches than from low-density food patches for most study plants (Fig. 1; Table 3), indicating that spiny pocket mice rapidly located rich food patches on the forest floor, as do other tropical heteromyid rodents (Sánchez-Cordero and Martínez-Gallardo 1998). Rapid fruit and seed removal from highly rewarding food patches coupled with hoarding or scatter-hoarding of food items in burrows or caches may result in decreasing predation risk and increasing foraging efficiency; this may explain why spiny pocket mice have small home ranges at Chamela compared with the home ranges of other tropical and desert heteromyids (Sánchez-Cordero and Fleming 1993). Alternatively, our failure to control for the abundance of naturally available fruits and seeds during the field experiments may have influenced the foraging and space use decisions of forest-dwelling mice in undetermined patterns, biasing our interpretations (Manson and Stiles 1998).

Community-level fruit and seed removal

The study plants, as well as other plants in tropical deciduous forests, produce massive crops of fruits and seeds, perhaps as an adaptive response to satiate predators and increase chances for seedling recruitment (Janzen 1971). In our studies, caged spiny pocket mice, *L. pictus*, were unable to maintain themselves solely by consuming fruits or seeds of most of the study plants in short-term monospecific feeding experiments (Briones and Sánchez-Cordero 1999). Consequently, spiny pocket mice should seek a wider diversity of fruits and seeds to acquire enough energy and nutrients.

Spiny pocket mice are known to gather a high diversity of fruits and seeds, with fruits and seeds of up to 84 plant species gathered, which represents 11% of the total vascular flora in Chamela (Lott et al. 1987, Briones 1996, Briones and Sánchez-Cordero 1999).

Spiny pocket mice are known to consume high quantities of fruits and seeds in Neotropical forests (Janzen 1971, 1982a, 1982b, 1986; Perry and Fleming 1980; Martínez-Gallardo and Sánchez-Cordero 1993; Sánchez-Cordero and Martínez-Gallardo 1998; Brewer and Rejmanek 1999; Briones and Sánchez-Cordero 1999). For example, spiny pocket mice deplete crops of several plants in tropical deciduous forest, such as seeds of the guanacaste *Enterolobium cyclocarpum* (Leguminosae) and *Crescentia alata* (Bignoniaceae) in Costa Rica (Janzen 1981, 1982a). Conversely, *Liomys* disregarded fruit and seed containing toxic metabolites, as in *Lonchocarpus eriocardinalis* and *Caesalpinia coriaria* (Leguminosae), in Chamela (Sánchez-Rojas et al. 2004). Our results suggest that plant species, habitat, and food density are not independent, and that a complex interplay between these factors determines rates of fruit and seed removal from the forest floor at the Chamela tropical deciduous forest (Tables 1 and 2).

Our study did not determine interannual variation in crop production and associated removal rates in study plants, thus limiting generalizations of observed patterns under more realistic spatiotemporal scenarios. Differences in both overall fruit and seed composition and availability in the forest floor, and spiny pocket mice abundance when experimental trials for the study plants were conducted in different months, could have influenced rates of seed removal (Manson and Stiles 1998). We consider, however, that the observed patterns of seed removal will hold even when removal rates change or when a larger set of plants producing large crops is tested, and these shortcomings pose questions for further research.

Post-dispersal removal results from complex foraging decisions by forest-dwelling rodents that preferentially select fruits and seeds containing high energy and (or) nutritional contents and disregard food items containing toxic metabolites from dense food patches in preferred habitats, and from a high diversity of plants (Janzen 1971, 1981, 1982a, 1982b, 1986; Smythe 1986; Forget 1993, 1996; Martínez-Gallardo and Sánchez-Cordero 1993; Forget et al. 1994, 1998; Sánchez-Cordero and Martínez-Gallardo 1998; Briones and Sánchez-Cordero 1999; Andrew et al. 2003; Sánchez-Rojas et al. 2004). If these results apply to other tropical deciduous forests, then observed nonrandom patterns in seedling recruitment result partially from complex foraging and space use decisions of forest-dwelling rodents.

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