

Effect of Plant Species, Fruit Density and Habitat on Post-Dispersal Fruit and Seed Removal by Spiny Pocket Mice (*Liomys pictus*, Heteromyidae) in a Tropical Dry Forest in Mexico

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Abstract

We tested whether quality, habitat, and food patch density affected post-dispersal fruit and seed removal of common plants in a tropical deciduous forest in western Mexico (Chamela, Jalisco). To identify the quality of seed or fruit, caged spiny pocket mice (*Liomys pictus*) were fed mono-specific diets of sunflower seeds (*Helianthus annuus*), seeds of *Delonix regia*, *Lonchocarpus eriocarinalis*, *Caesalpinia coriaria*, or fruits of *Spondias purpurea*. Caged mice gained weight with sunflower seeds, marginally lost weight with *D. regia* seeds, and significantly lost weight with *S. purpurea* fruits and *L. eriocarinalis* and *C. coriaria* seeds. Fruit and seed removal values in experimental patches were high in sunflower (80%) and *D. regia* (70%) seeds, and moderate in *S. purpurea* fruits (50%); *L. eriocarinalis* (0.1%) and *C. coriaria* (0%) seeds were not removed. More fruits and seeds were removed from experimental patches in tropical deciduous forest (57%) than from semi-deciduous forest (23%), and from high (43%) and medium density (46%) than from low density (31%) food patches. Similar fruit and seed removal values from experimental patches open either to all removal agents or open only to forest-dwelling rodents, suggest that spiny pocket mice were important removal agents of tested plants. Spiny pocket mice food choices can influence observed non-random patterns in seedling recruitment.

Resumen

Se probó si la remoción post-dispersión de frutos y semillas de plantas comunes en el bosque tropical deciduo de México (Chamela, Jalisco), es afectada por su calidad, el hábitat ó la densidad en la que se depositan. Para determinar su calidad, se efectuaron experimentos en el laboratorio en los roedores con abazones (*Liomys pictus*), sujetos a dietas mono-específicas de semillas de girasol (*Helianthus annuus*), de *Delonix regia*, *Lonchocarpus eriocarinalis*, *Caesalpinia coriaria* y frutos de *Spondias purpurea*. Los roedores mantuvieron su peso con dietas de semillas de girasol, mostraron un ligero decremento de peso con dietas de semillas de *D. regia*, y mostraron un decremento significativo con semillas de *L. eriocarinalis* y *C. coriaria* y frutos de *S. purpurea*. La remoción post-dispersión en parcelas experimentales fue alta en semillas de girasol (80%) y de *D. regia* (70%), moderada en frutos de *S. purpurea* (50%), e insignificante en frutos de *L. eriocarinalis* (0.1%) y *C. coriaria* (0%). Los frutos y semillas mostraron valores de remoción más altos en el bosque tropical deciduo (57%) que en el bosque semi-deciduo (22.5%), y en las parcelas con densidades altas (42.8%) y medias (45.9%), que en las de densidad baja (30.6%). Se observaron valores similares de remoción en las parcelas abiertas a todos los agentes removedores y en las que los frutos y semillas estaban disponibles sólo a los roedores, lo

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que sugiere que *L. pictus* fue el removedor más importante de las plantas probadas. La remoción selectiva de frutos y semillas de *L. pictus* puede influir en la tendencia no aleatoria del reclutamiento de plántulas en este bosque tropical deciduo.

Keywords: Spiny pocket mice, *Liomys pictus*, tropical deciduous forest, foraging behavior, seed predation, Mexico.

Introduction

Post-dispersal removal of fruits and seeds is a major cause of seed mortality (Janzen, 1969, 1971; Brown et al., 1979; Schupp, 1988a,b; Wilson & Whelan, 1990). High post-dispersal fruit and seed removal rates can have a direct impact on an individual's reproductive success, affecting the population and community structure of plants (Howe & Smallwood, 1982; Price & Jenkins, 1986). Research on post-dispersal seed predation has focused mainly on the consequences on seedling survival, investigating the effect of plant species, food patch densities, and habitats on post-dispersal fruit and seed removal (Janzen, 1969, 1971, 1986).

Terrestrial mammals are known to consume large quantities of the fruits and seeds that fall to the floor in Neotropical forests. Research has shown that these mammals prefer fruits and seeds with a high energy and nutritional content, disregard those containing toxic metabolites (Janzen, 1971, 1986), select high density over low density food patches (Brown & Mitchell, 1989), and forage preferentially in low rather than high risk habitats (Smythe, 1986). Several studies have demonstrated that forest-dwelling rodents are important post-dispersal fruit and seed removal agents (Janzen, 1971, 1981, 1982a,b, 1986; Schupp, 1988a,b; Forget, 1996; Sánchez-Cordero & Martínez-Gallardo, 1998; Brewer & Rejmanek, 1999), and their activity as seed removal agents has an important indirect effect on the changes in the density and horizontal heterogeneity of understory vegetation (Malcom, 1995). To understand non-random patterns of post-dispersal seed removal it is essential to gain a better knowledge of the foraging behavior of seed predators (Janzen, 1981, 1982a,b, 1986).

Spiny pocket mice of the genus *Liomys* are prominent removal agents because they consume a great diversity of fruits and seeds, and reach high densities in tropical deciduous forests (Janzen, 1981, 1986; Sánchez-Cordero & Fleming, 1993; Briones, 1996). In the tropical forest of Chamela (western Mexico), spiny pocket mice were found to be the most abundant terrestrial mammals, perhaps acting as the major post-dispersal fruit and seed removal agents (Ceballos, 1990; Briones, 1996). Spiny pocket mice gather a high diversity of fruits and seeds (84 species, comprising approximately 11% of the vascular flora at Chamela) in their cheek-pouches (Sánchez-Cordero & Fleming, 1993).

Previous work has been based on the hypothesis that those fruits and seeds that increase or maintain rodent body weight in mono-specific feeding trials will have higher removal rates than those fruits or seeds that cause a decrease in rodent weight (Martínez-Gallardo & Sánchez-Cordero, 1993; Briones & Sánchez-Cordero, 1999). In this study, we tested that hypothesis using four plant species which produce large crops in Chamela: *Spondias purpurea* (Anacardiaceae), *Delonix regia*, *Caesalpinia coriaria*, and *Lonchocarpus eriocarinalis* (Leguminosae). Sunflower seeds (*Helianthus annuus*) were used as a control. We estimated the influence of each plant species, food patch density and habitat on post-dispersal fruit and seed removal, and evaluated the relative importance of spiny pocket mice and other vertebrates in removing these plants from the Chamela forest floor.

Materials and methods

Study area

The study site is located at the Chamela Biological Station of the Instituto de Biología, Universidad Nacional Autónoma de México, on the coast of Jalisco, Mexico (105°5'W, 19°33'N; elevation 150–530 m). Mean annual temperature is 25°C, with May through September being the hottest months of the year. Mean annual precipitation is 748 mm, with 80% of the rain falling during July to November; the dry season extends from December to June, with a monthly precipitation below 50 mm (Bullock, 1988). The dominant vegetation is tropical deciduous forest (TDF), covering 75% of Chamela; the dominant trees species are *Cordia alliodora* (Boraginaceae), *Lonchocarpus lanceolatus* and *Caesalpinia eriostachys* (Leguminosae). Chamela also includes a tropical semi-deciduous forest (TSF), with trees ranging from 10–25 m in height. This vegetation type is usually found along main streams and in protected places on deep soil. The dominant trees in this vegetation type are *Astronium graveolens* (Anacardiaceae), *Brosimum alicastrum* (Moraceae) and *Sideroxylon capiri* (Sapotaceae) (Lott et al., 1985). All species used in this study, except sunflower seeds, occur in both types of vegetation.

Feeding trials in the laboratory

Adult spiny pocket mice (30–45 g) were live-trapped during the dry season (April–June) of 1990 using folding Sherman traps (8 × 9 × 23 cm). Mice were housed individually in cages (60 × 30 × 20 cm), and fed with sunflower seeds and water *ad libitum* for five days prior to experiments. Fresh fruits of *S. purpurea*, and seeds of *D. regia*, *C. coriaria*, and *L. eriocarinalis* were collected from the forest floor and stored in a freezer. Spiny pocket mice are known to gather whole or parts of fruits and seeds of these species (Briones & Sánchez-Cordero, 1999). Because of their known high nutritive quality sunflower seeds were included in the experiments to test whether the captive condition or the manipulation of the

mice while weighing them were the causes of a decrease in body weight during the experiment. Mice maintained or gained weight during periods of 10 days in captivity when fed sunflower seeds (M. Briones, personal observation).

Mice were assigned to five groups of six individuals each (totaling 30 individuals) for the feeding trials. Each group was fed with 30 g/day/animal of a different fruit or seed diet from the five species of plants during five consecutive days and water was provided *ad libitum*. Cages were cleaned daily (1600–1800 h), and the mice and food residuals were weighed before adding a fresh portion of fruits or seeds (see Briones & Sánchez-Cordero, 1999). Whenever mice showed signs of weakness such as shaking and trembling, they were immediately removed from the experiment.

We used a randomized one-way ANOVA and the least significance difference test (LSD) to compare the differences in initial and final weight of mice fed with different diets (Sokal & Rohlf, 1995). Results are presented as mean \pm standard deviation of the percent variation in mouse weight.

Fruit removal experiments in the field

All field removal experiments were conducted in the late dry season (April–May) of 1990. Fresh fruits and seeds were collected as above, and sunflower seeds were also included. To test for the influence of plant species and fruit density on removal, 72 single-species patches of fruits or seeds in three densities (low: 5, medium: 25, high: 50) were established on squares of soil (25 cm \times 25 cm) cleared from litter. In order to examine whether small rodents act as the main removal agents, half of the food patches (36) were surrounded with a semi-permeable enclosure using a mesh-wire cage staked to the ground, with one 3 cm wide opening between the bottom of the cages and the ground, thus restricting access to small rodents only (i.e. the Spiny pocket mouse, *Liomys pictus*; Marsh mouse, *Peromyscus perfulvus*; and Michoacan deer mouse, *Osgoodomys banderanus*); the other half of the food patches were not surrounded by any enclosure, making them freely accessible to all removal agents. To test for the influence of vegetation type, we set up 36 of the food patches (12 per density, six per treatment, i.e. enclosure vs. non-enclosure) in each of both forest types (TDF and TSF). The 72 experimental food patches (six replicates per three densities per two treatments per two types of vegetation) for each of the five plants species were randomly distributed. Sand beds (25 cm \times 25 cm) were placed besides each food patch to record the tracks of the potential seed and fruit removing agents. In addition, direct observations from sunset to midnight using a red light helped identify potential removal agents visiting the experimental food patches.

We used the percentage of fruits and seeds removed after five days to investigate the effect on fruit and seed removal by each factor with a multiple ANOVA (Zar, 1999). We performed an arcsine transformation on the percentage of fruit and seed removal after five days for the ANOVA.

Results

Feeding trials in the Laboratory

Mouse consumption of sunflower and *D. regia* seeds was between 30–60% of the total amount offered. The consumption of *S. purpurea* was ca. 80% of the offered quantity, and in the case of *L. eriocarinalis* and *C. coriaria*, mice only ate between 10–30% of the offered food. For the *L. eriocarinalis* fruits, mice only ate the embryo, while for the other four species all parts were consumed. Caged mice gained weight with sunflower seeds ($4.7 \pm 11.5\%$), slightly lost weight with *D. regia* seeds ($-1.3 \pm 4.7\%$), and lost significant weight with fruits of *S. purpurea* ($-18.1 \pm 2.9\%$), and seeds of *L. eriocarinalis* ($-15.4 \pm 15.7\%$), and *C. coriaria* ($-16.9 \pm 4.9\%$). There was a significant difference in mouse weight between tested fruits and seeds ($F = 7.51$, d.f. = 4, $P < 0.001$); all pairwise multiple comparison procedures (LSD) showed that mice fed with seeds of *H. annuus* and *D. regia* lost significantly less weight than with mice fed with fruits of *L. eriocarinalis*, *S. purpurea* and *C. coriaria*.

Fruit removal experiments in the field

There was no significant difference in fruit and seed removal between non-enclosed and semi-permeable enclosures (36.88% in non-enclosed and 37.1% in semi-permeable enclosure) so this factor was excluded from further analyses. On average, *Helianthus annuus* (80.5%) and *D. regia* (69.0%) seeds were removed in high proportions, *S. purpurea* (49.3%) fruits in moderate proportions, whereas *L. eriocarinalis* (0.1%), and *C. coriaria* (0%) seeds were not removed (Table 1). Fruit or seed removal in the field was significantly higher in TDF (57.0%) than in TSF (22.5%) ($F = 121.079$, d.f. = 1, $P < 0.001$), and significantly higher in high (42.8%) and medium (45.9%) compared with low (30.6%) density food patches ($F = 7.317$, d.f. = 2, $P < 0.001$). For *S. purpurea* in TDF and for sunflower and *D. regia* in TSF, fruit and seed removal was density-dependent. A three-way ANOVA using species, habitat and density as factors showed that removal values between fruits and seeds were significantly different ($F = 140.648$, d.f. = 4, $P < 0.001$) (Table 2). There was a significant interaction between plant species and habitat ($F = 22.102$, d.f. = 4, $P < 0.001$) and plant species and food patch density ($F = 3.092$, d.f. = 8, $P = 0.005$) (Table 2).

Seventy percent of the tracks in the sand beds in both, the non-enclosure and the semi-permeable food patches, belonged to spiny pocket mice and all direct observations were of *L. pictus* ($N = 16$).

Discussion

The results of the laboratory feeding trials suggest that sunflower and *D. regia* are energetically and nutritionally rich seeds for spiny pocket mice, since individuals fed with these

Table 1. Influence of forest type and density on fruit and seed removal in 72 experimental food patches of five plant species at three different densities (low: 5, medium: 25, high: 50) at the Chamela Biological Station, Jalisco, Mexico. Mean \pm standard deviation (in %) of 12 replicates per treatment are shown.

Plant species	Seeds removed after 5 days					
	Tropical deciduous forest			Tropical semi-deciduous forest		
	low	medium	high	low	medium	high
<i>Helianthus annuus</i>	100	98.7 \pm 4.6	100	25 \pm 45.2	72.5 \pm 45.2	77.1 \pm 33
<i>Delonix regia</i>	95.5 \pm 15	100	100	25 \pm 45	58.3 \pm 51	41.7 \pm 51
<i>Spondias purpurea</i>	58.3 \pm 51	100	91.7 \pm 2.8	25 \pm 45	25 \pm 45.2	20.8 \pm 39
<i>Lonchocarpus eriocarinalis</i>	0	0	0	0	0	2 \pm 3
<i>Caesalpinia coriaria</i>	0	0	0	0	0	0

Table 2. Results of three-way ANOVA comparing removal of tested fruits and seeds, depicting effects of species (five plant species), habitat (tropical deciduous forest and tropical semi-deciduous forest) and density of food patches (low: 5, medium: 25, high: 50 fruits or seeds).

Source of variation	Degree of freedom	Sum square	Mean square	F value	P value
Species	4	101.707	25.427	140.648	<0.001
Habitat	1	21.883	21.883	121.079	<0.001
Density	2	2.645	1.322	7.317	<0.001
Species \times Habitat	4	15.979	3.995	22.102	<0.001
Species \times Density	8	2.091	0.261	1.446	0.176
Habitat \times Density	2	0.222	0.111	0.613	0.542
Species \times Habitat \times Density	8	4.470	0.559	3.092	0.002
Residual	330	59.643	0.181		
Total	359	208.640	0.581		

diets increased or maintained their weight. Therefore, we predicted a high seed removal rate for both plant species (see Briones & Sánchez-Cordero, 1999). In contrast, the loss of weight and the evidence of weakness in individuals fed solely with *S. purpurea* fruits and *L. eriocarinalis* and *C. coriaria* seeds may indicate poor energetic and nutritional values, or the presence of toxic metabolites deterrent to spiny pocket mice. Thus a low removal rate for these seeds should be expected and except for *S. purpurea*, our results agreed with these predictions. Bora et al. (1991) reported that fruits of *S. mombin*, a species very closely related to *S. purpurea*, have low energetic and nutritional value (87% water, 5% sugar, and 0.2% protein for pulp alone). There is indirect evidence that this is also true for *S. purpurea*, since spiny pocket mice were not able to maintain their weight with that diet alone, although they readily consumed most of the frozen pulp and seeds offered to them in the feeding trials. So the moderate removal rate is perhaps due to their sugar and water content, since both resources are very scarce during the dry season in Chamela (Bullock & Solis-Magallanes, 1990; Mandujano et al., 1994).

Density dependence of fruit and seed removal suggest that animals might be responding to a 'giving up' density

(see Brown & Mitchell, 1989), as found in other tropical heteromyids (Sánchez-Cordero & Martínez-Gallardo, 1998). It is possible that that seed removal was much higher in the TDF than in the TSF because the density of *Liomy pictus* in TDF is higher (Ceballos, 1990). Additionally, differences in removal values between habitats may be attributed to differences in predation risk (Brown, 1989). Ocelots (*Leopardus pardalis*) prey on spiny pocket mice and are more commonly found in TSF than in TDF at Chamela (Devilla et al., 2002).

Our results show that plant species, habitat type and patch density are not independent parameters and that a complex interplay between the factors influences post-dispersal fruit and seed removal in Neotropical deciduous forest (Schupp, 1988a,b). Differences in removal patterns among plant species by rodents have been observed elsewhere in temperate deciduous forest of central Illinois (Wilson & Whelan, 1990) and can be attributed to a foraging behavior of seed predators that results from complex decision making by evaluating costs and benefits of food qualities, and responds to temporal and spatial variations in food availability as well as immediate individual necessities (more thirst or more hunger). This spatio-temporal variation must be considered

in future studies in order to understand the effects of removal in a seed dispersal system (Ortiz-Pulido & Rico-Gray; 2000).

The footprint records on the sand beds in Chamela support our assumption that spiny pocket mice are the main predators of fruits and seeds. This finding agrees with observations from other studies that suggest that spiny pocket mice are important removal agents in Neotropical dry forests (Janzen, 1981, 1982a; 1986, Sánchez-Cordero & Fleming, 1993; Sánchez-Cordero & Martínez-Gallardo, 1998; Brewer & Rejmanek, 1999). If such non-random patterns of post-dispersal fruit and seed removal occur for other plants, then differences in seedling recruitment may be partially determined by the foraging behavior of spiny pocket mice in tropical dry forests.

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