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# Postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico

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ABSTRACT. This study examined whether postdispersal fruit and seed removal by terrestrial mammals of common plant species was affected by the type of item, item density (low, medium, high), and habitat (gap, mid-succession, mature). Fruits of *Brosimum alicastrum* and *Ficus yoponensis* (Moraceae), *Astrocaryum mexicanum* (Palmae), and *Nectandra ambigens* (Lauraceae), and seeds of *Omphalea oleifera* (Euphorbiaceae) and *Cymbopetalum baillonii* (Annonaceae) were tested at the Los Tuxtlas rainforest in Mexico. Item removal from 108 experimental patches (N = 2340 fruits or seeds for each plant species tested) after 5 d was lower for *F. yoponensis* (6.6%) than for *N. ambigens* (68.8%), *B. alicastrum* (67.8%) *C. baillonii* (64.0%) and *A. mexicanum* (60.0%). No seeds of *O. oleifera* were removed. A higher fruit or seed removal was observed from high density than low density food patches in *A. mexicanum*, *C. baillonii* and *N. ambigens*, but not in *B. alicastrum* and *F. yoponensis*. A higher fruit or seed removal was observed from food patches in mature forest than in gaps in all plant species tested. Similar removal values between open (open to all terrestrial mammals) and caged (open to small rodents) fruit and seed patches, abundant rodent live-trapping, and a scarcity of large terrestrial mammals, indicated that forest-dwelling small rodents were the main postdispersal removal agents. Differences in plant species seedling recruitment resulting from small rodent food choices can partially determine long-term forest floristic composition at the Los Tuxtlas rainforest.

RESUMEN. Se determinó si la remoción postdispersión de frutos y semillas de plantas comúnes, por parte de los mamíferos terrestres, es afectada por la especie de planta, la densidad de los lotes de frutos ó semillas y por el hábitat (claro, sucesión secundaria y selva madura). Frutos de *Brosimum alicastrum* y *Ficus yoponensis* (Moraceae), *Astrocaryum mexicanum* (Palmae) y *Nectandra ambigens* (Lauraceae) y semillas de *Omphalea oleifera* (Euphorbiaceae) y *Cymbopetalum baillonii*

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(Annonaceae) fueron sujetos a los experimentos en la selva húmeda de Los Tuxtlas, México. La remoción de frutos ó semillas colocados en 108 lotes experimentales (N = 2340 frutos ó semillas de cada especie) después de cinco días, fue menor en *F. yoponensis* (6.6%) que en *N. ambigens* (68.8%), *B. alicastrum* (67.8%), *C. baillonii* (64.0%) y *A. mexicanum* (60.0%). Ninguna semilla de *O. oleifera* fue removida. Se observó una mayor remoción en lotes con alta densidad de frutos ó semillas que en lotes de baja densidad en *B. alicastrum*, *C. baillonii* y *A. mexicanum*, aunque esta diferencia no se observó en *N. ambigens* y *F. yoponensis*. Se observó una mayor remoción en lotes de frutos ó semillas colocados en selva madura que en lotes colocados en los claros en todas las especies de plantas consideradas. Valores similares de remoción en lotes con protección (disponibles sólo a roedores) y en lotes sin protección (disponibles a todas las especies de mamíferos terrestres), trampeos frecuentes de roedores y una notoria ausencia de mamíferos de talla mediana y mayor, sugieren que los pequeños roedores son los agentes más importantes en la remoción postdispersión de estas especies de frutos y semillas. Las diferencias en el reclutamiento de plántulas que resulten de la selección de frutos y semillas por roedores puede determinar parcialmente a largo plazo, la composición florística de Los Tuxtlas.

KEY WORDS: Ecology, fruits, forest-dwelling rodents, granivory, terrestrial mammals, Mexico, postdispersal, rainforest, seeds.

## INTRODUCTION

In Neotropical forests, fruits and seeds fallen from trees are consumed by a guild of frugivores. Terrestrial mammals remove many of these food items and constitute important postdispersal fruit and seed removal predators and/or dispersers (Forget & Milleron 1991, Janzen 1971, Smythe 1986, Terborgh *et al.* 1993). Since postdispersal seed removal may ultimately determine the fate of seeds, it should have a major impact on individual reproductive success of plants, spatial distribution and community structure of many plant species (Howe & Smallwood 1982, Price & Jenkins 1986).

Several studies have noted contrasting patterns of postdispersal seed removal that may be attributed to differences in the foraging behaviour of terrestrial mammals. First, the intensity of postdispersal seed removal may depend on the fruit or seed species (Janzen 1971). Terrestrial mammals, such as small forest-dwelling rodents, showed marked feeding preferences for fruits and seeds with a high energy and/or nutritional content, and avoided those containing toxic compounds (Janzen 1970, 1971, 1986; Martínez-Gallardo & Sánchez-Cordero 1993, Smythe 1986).

Second, postdispersal seed removal may be density-dependent (Janzen 1970). Dense patches of fruits and seeds, usually occurring below fruiting parent trees, are predicted to suffer disproportionately high removal compared to less dense patches because they are more profitable for foragers (Janzen 1970, 1971). Third, postdispersal seed removal may be habitat-dependent (Schupp 1988a,b). Contrasting fruit and seed removal in different rainforest microhabitats (e.g. in gaps *vs* mature forest understorey; see Schupp 1988a,b, 1990; Schupp *et al.*

1989, Smythe 1986) and tropical deciduous forest (e.g. secondary successional forests; see Janzen 1982, 1986) have been attributed to high mammalian feeding activity in these particular microhabitats.

Studies at the Los Tuxtlas rainforest in Mexico have documented rapid post-dispersal removal of seeds of several plant species by terrestrial mammals (Coates-Estrada & Estrada 1988, Dirzo & Domínguez 1986; Estrada & Coates-Estrada 1986, 1991; Estrada *et al.* 1993). In a previous study, we predicted postdispersal fruit and seed removal by small forest-dwelling rodents for several plant species based on fruit and seed dietary values when tested in laboratory monospecific-diet feeding trials. *Nectandra ambigens*, *Brosimum alicastrum* and *Astrocaryum mexicanum* fruits and *Cymbopetalum baillonii* seeds were highly profitable compared with *Ficus yoponensis* fruits and mice did not consume *Omphalea oleifera* seeds (Martínez-Gallardo & Sánchez-Cordero 1993). Here, we compared removal rates for these co-existing common plant species that produce large crops at Los Tuxtlas. We examined immediate feeding responses by terrestrial mammals since these seeds can quickly germinate after fruitfall (< 1 mo), or suffer rapid deterioration due to pathogens (Estrada & Coates-Estrada 1986, 1991; V. Sánchez-Cordero & R. Martínez-Gallardo, *pers. obs.*). Specifically, we tested whether postdispersal fruit and seed removal was related to the species of fruit or seed, density, and/or habitat. We further evaluated the relative importance of small forest-dwelling rodents (< 0.15 kg) and medium-to-large terrestrial mammals (> 0.30 kg) as fruit and seed removal agents at Los Tuxtlas.

## METHODS

This study was conducted at the Estación de Biología Tropical Los Tuxtlas of the Instituto de Biología, Universidad Nacional Autónoma de México, located in southern Veracruz, Mexico. The dominant vegetation type is tall evergreen lowland rainforest. The climate is hot and humid with a mean annual temperature of 25 °C (range = 22–27 °C), an annual precipitation of 4900 mm (range = 4200–5400 mm), and an elevation of 500 m. The rainy season begins in mid-June and lasts through February, with heavy rains occurring in August, September and October. The dry season begins in March and extends through May, although even during that period each month averages usually more than 100 mm of precipitation (Ibarra & Sinaca 1987).

We chose fruits or seeds of six common plant species at Los Tuxtlas that produce large crops leading to dense and conspicuous seed shadows. Fruits of *B. alicastrum* (Moraceae) (mean ± SE length = 1.9 ± 0.2 cm, n = 100), *F. yoponensis* (Moraceae) (1.6 ± 0.3 cm, n = 100), *A. mexicanum* (Palmae) (6.2 ± 1.2 cm, n = 100), and *N. ambigens* (Lauraceae) (2.4 ± 0.3 cm, n = 100) collected in July, October and December of 1986, and January of 1987, respectively, and seeds of *O. oleifera* (Euphorbiaceae) (2.5 ± 0.2 cm, n = 100 seeds), and *C. baillonii*

(Annonaceae) (1.5 ± 0.1 cm) collected in May and June of 1987, respectively, were included in the experimental protocols.

Fresh fruits or seeds were collected from the forest floor during fruit fall peaks. The removal experiments were conducted late during the fruiting season of each plant species, when considerable postdispersal fruit and seed removal had already occurred. We placed single-species fruit or seed patches on squares (25 cm × 25 cm) of ground cleared of litter. Two treatments were applied for both fruit and seed density- and habitat-dependent removal experiments: (1) partial exclosure, protected with a mesh-wire cage staked down to the ground. One 3 cm opening between the cage's bottom and the ground provided access to only small forest-dwelling rodents (i.e. spiny pocket mice *Heteromys desmarestianus* and Mexican deermice *Peromyscus mexicanus*); (2) non-exclosure, allowing direct access to all terrestrial mammals. There was evidence that these large fruits and seeds were removed by arthropods, and no attempt was made to exclude them.

We located fruit or seed patches randomly in the experimental plots (see description thereafter) for each fruit or seed species tested. Fruit or seed removal from patches was monitored for five consecutive days for each treatment. Both density- and habitat-dependent seed removal experiments were conducted simultaneously for each plant species tested.

### *Density dependence*

We conducted the density-dependent seed removal experiments on mature forest habitat. Six replicates for each low (five fruits or seeds), medium (15) and high (45) patch density were established for both treatments, totalling 108 patches with 2340 fruits or seeds per species.

### *Habitat-dependence*

We conducted the habitat-dependent seed removal experiment in three habitats: gap, mid-succession and mature forest. We set 0.25 ha plots in two gaps, two mid-succession and two mature forest habitats, totalling six plots. Thirty-six replicates of 15 fruit or seed patches were placed on each plot for both treatments, totalling 216 patches with 3240 fruits or seeds. We chose natural tree-fall gaps, with 15–30 $m^2$ open canopy; mid-succession with 10 to 20 y of natural regeneration from former gaps; and mature forest with no evidence of natural disturbance (e.g. treefalls) for at least 30 y (Martínez-Ramos, *pers. comm.*). Reliable dating of habitat disturbances at Los Tuxtlas is possible from population studies of selected palm and tree species (Martínez-Ramos *et al.* 1989). These habitats contrast in their floristic structure and species composition, with pioneer and shade-tolerant plant species found predominantly in gaps and mature forest, respectively (Martínez-Ramos *et al.* 1989).

### *Mammal records*

To record tracks of terrestrial mammals, we placed 10 sandbeds (1 m × 1 m) per plot (total = 30) and 20 smoked index cards (0.1 m × 0.1 m) per plot (total =

60) for the density-dependent experiments, and five sandbeds (1 m × 1 m) per plot (total = 30) and 20 smoked index cards (0.1 m × 0.1 m) per plot (total = 120), for the habitat-dependent experiments, circling randomly chosen experimental patches. After completion of the 5-d density-dependent and habitat-dependent experiments, all fruits or seeds from the two treatments were removed. We then set 40 Sherman traps per plot spaced at 5-m intervals (total = 120 traps), baited them with oatmeal for three consecutive nights for trapping mice.

### *Statistical analyses*

The percentage of fruits or seeds removed from patches was arcsine-transformed for statistical analysis. Analysis of variance (ANOVA) was used to compare fruit or seed removal for each plant species for the density-dependent (density, treatment and interaction), and habitat-dependent (habitat, treatment and interaction) experiments. Bartlett's test was not significant indicating homogeneity of variances ($P = 0.90$ to 0.97; Zar 1984).

## RESULTS

Percentage removal (± 95% C.I.) after 5 d did not differ between *N. ambigens* (68.8 ± 3.5%), *B. alicastrum* (67.8 ± 5.2%), *C. baillonii* (64.0 ± 5.5%), and *A. mexicanum* (60.0 ± 10.1%), but was significantly lower for *F. yoponensis* (6.6 ± 4.8%) ($F = 50.7$; $P < 0.0001$, $n = 2340$ fruits and seeds). No seeds of *O. oleifera* were removed and this plant species was excluded in further analyses.

### *Exclosure treatment*

Fruit or seed removal did not differ between exclosure and non-exclosure treatments for each plant species tested in the density-dependent and habitat-dependent removal experiments (Tables 1 & 2).

Table 1. Analyses of variance indicating the effect of patch density (low, medium and high), with and without exclosure, on the postdispersal fruit and seed removal of common plant species by terrestrial frugivorous mammals at the Los Tuxtlas rainforest, Mexico.

| | | F-ratio[1] | |
|---|---|---|---|
| | Density | Treatment | Interaction |
| df | 2 | 1 | 2 |
| *Brosimum alicastrum* | 1.49 | 1.14 | 0.58 |
| *Ficus yoponensis* | 0.30 | 0.25 | 0.27 |
| *Astrocaryum mexicanum* | 6.17** | 0.00 | 0.67 |
| *Nectandra ambigens* | 2.50 | 0.24 | 0.26 |
| *Cymbopetalum baillonii* | 4.20* | 0.17 | 0.09 |

[1] Error df = 30

* $P < 0.05$; ** $P < 0.005$.

### *Density-dependent seed removal*

Fruit or seed removal differed significantly from high and medium density patches compared with low density patches in *A. mexicanum*, *C. baillonii* and *N.*

Table 2. Analyses of variance indicating the effect of habitat (gap, mid-succession and mature forest), with and without exclosure on the postdispersal fruit and seed removal of common plant species by terrestrial frugivorous mammals at the Los Tuxtlas rainforest, Mexico.

| | | F-ratio[1] | |
|---|---|---|---|
| | Habitat | Treatment | Interaction |
| df | 2 | 1 | 2 |
| *Brosimum alicastrum* | 16.42*** | 1.68 | 0.54 |
| *Ficus yoponensis* | 2.87 | 0.96 | 0.26 |
| *Astrocaryum mexicanum* | 8.88** | 1.02 | 0.29 |
| *Nectandra ambigens* | 8.88** | 1.02 | 0.29 |
| *Cymbopetalum baillonii* | 5.24* | 1.31 | 0.06 |

[1] Error df = 66

* $P$ <0.01; ** $P$ <0.001; *** $P$ <0.0001.

*ambigens*, but no differences in fruit removal between *B. alicastrum* density patches were observed. Fruits of *F. yoponensis* were removed more from low compared with high (50% of total; Figure 1) density patches. The density × treatment interaction was not significant for any plant species tested (Table 1).

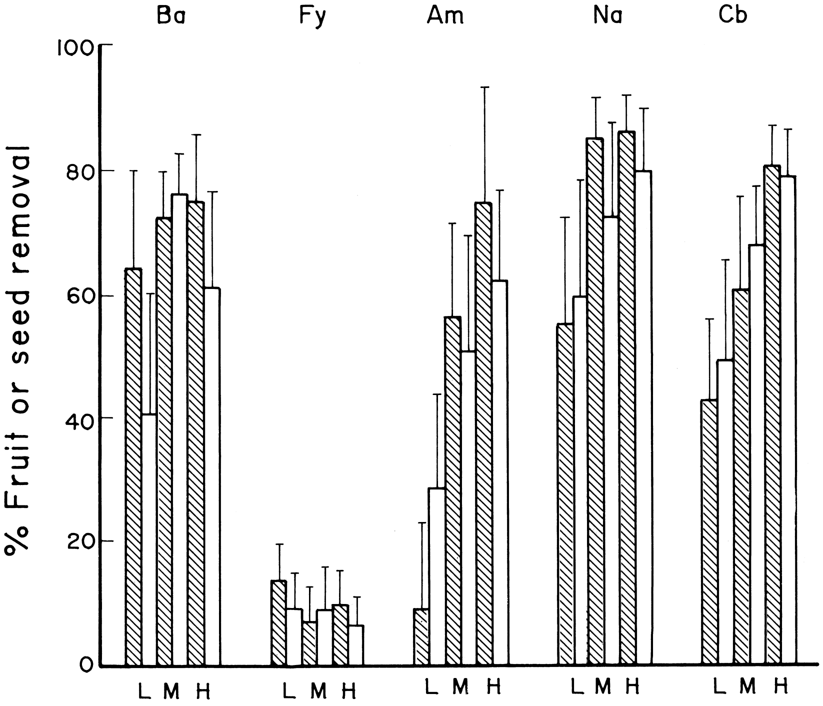

Figure 1. Postdispersal fruit and seed removal for the plant species tested in exclosure and non-exclosure treatments (± SE) for density-dependent experiments. Only forest-dwelling rodents had access to fruit or seed patches in the exclosure treatment, and all terrestrial mammals had access to fruit or seed patches in the non-exclosure treatment. Abbreviations of plant species tested: Ba, *Brosimum alicastrum*; Fy, *Ficus yoponensis* (Moraceae); Am, *Astrocaryum mexicanum* (Palmae); Na, *Nectandra ambigens* (Lauraceae); Cb, *Cymbopetalum baillonii* (Annonaceae). X-axis labels correspond to L: low (five fruits or seeds/patch), M: medium (15) and H: high (45) density patches.

### *Habitat-dependent seed removal*

Fruit or seed removal was significantly lower in gaps compared with mid-succession and mature forest habitats in all plant species tested (Table 2, Figure 2). Fruits of *B. alicastrum* and *A. mexicanum* were also removed more from mature forest compared with mid-succession habitats (LSD test, $P < 0.05$). Fruit removal in *F. yoponensis* was not significantly different among habitats (Figure 2). The habitat × treatment interaction was not significant for any plant species tested (Table 2).

Tracks of large terrestrial mammals were recorded occasionally during removal experiments particularly those with fruits of *B. alicastrum* and *F. yoponensis* (Table 3). Spiny pocket mice *Heteromys desmarestianus* and Mexican deermice *Peromyscus mexicanus* abundance was high and tracks were common during *C. baillonii*, *B. alicastrum* and *A. mexicanum* density- and habitat-dependent seed removal experiments. The lowest mice abundance and track records were observed after completion of *O. oleifera* seed removal experiment (Table 4).

## DISCUSSION

We expected a higher postdispersal fruit and seed removal in non-exclosure treatments since these patches were exposed to both small forest-dwelling rodents and large terrestrial mammals. Similar values between exclosure and non-exclosure treatments for both experiments suggest that small forest-dwelling rodents were the main postdispersal seed removal agents for the plant species tested. The few track records of large terrestrial mammals on the experimental plots suggested virtually no activity within the fruit and seed patches. We tested whether the fruit and seed types used were unpalatable to large terrestrial mammals to explain the surprising lack of feeding activity. Captive agoutis *Dasyprocta mexicana*, pacas *Agouti paca* and collared peccaries *Tayassu tajacu* readily consumed samples of the fruits and seeds tested, except *O. oleifera* seeds (Martínez-Gallardo & Sánchez-Cordero 1997).

The low frequency of track records within experimental plots supports earlier studies documenting abnormally low populations of most large terrestrial mammal species at the Los Tuxtlas rainforest (Estrada *et al.* 1993). Of a total of 26 terrestrial mammal species reported as potential fruit and seed removal agents, only 13 (50%) small-to-medium size species were recorded on sandbeds and/or smoked index cards during the experiments (Table 3). Overhunting and loss of pristine habitat have led Los Tuxtlas to a contemporary defaunation producing low rates of herbivory (Dirzo & García 1992, Dirzo & Miranda 1992). In our study, abundant live-trapping and track records of spiny pocket mice and Mexican deermice on experimental plots and additional signs of consumed fruit and seeds, indicated intensive mouse feeding activity on fruit and seed patches.

Populations of large terrestrial frugivorous mammals at Los Tuxtlas are presently reduced (Estrada *et al.* 1993; Martínez-Gallardo & Sánchez-Cordero

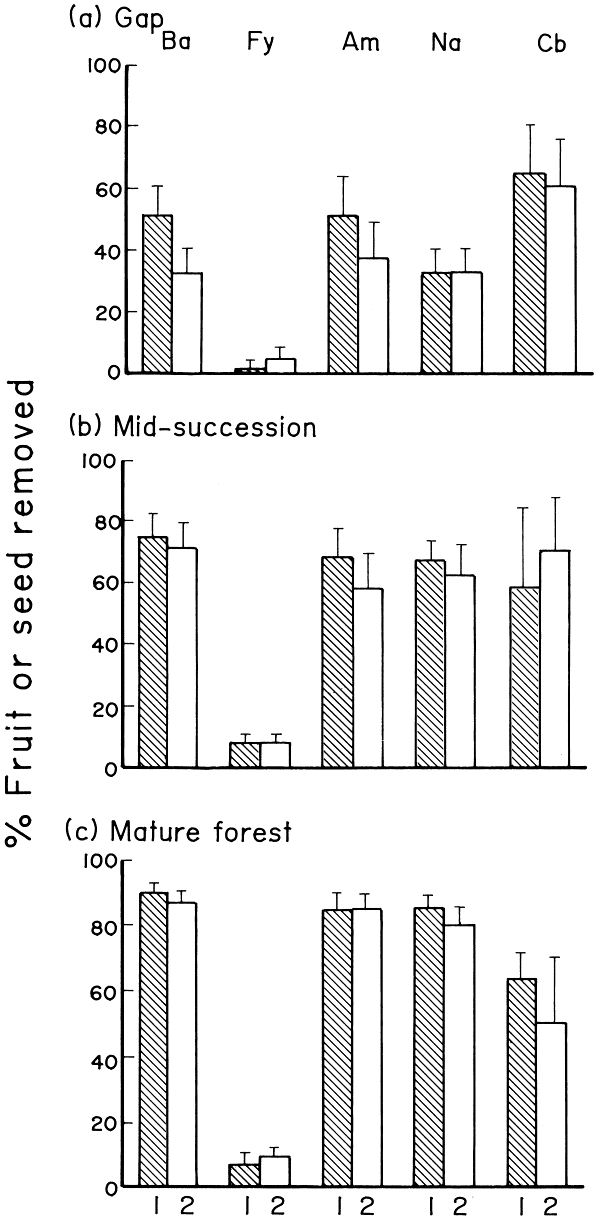

Figure 2. Postdispersal fruit and seed removal for the plant species tested in exclosure and non-exclosure treatments (+ SE) for the habitat-dependent experiments. Access to fruits or seed patches in treatments were as in the density-dependent experiments. Abbreviations of plant species tested are the same as in Figure 1. X-axis numbers 1 and 2 refer to the two sites studied for each of three habitat types: gap, mid-succession and mature forest.

Table 3. Terrestrial mammal tracks detected on sandbeds and/or smoked index cards recorded during both density-dependent and habitat-dependent experiments for each fruit and seed type tested at the Los Tuxtlas rainforest.

| | Plant species[1] | | | | | |
|---|---|---|---|---|---|---|
| Terrestrial mammal | Ba | Fy | Am | Na | Cb | Oo |
| *Didelphis marsupialis* | X | X | X | X | X | X |
| *Philander opposum* | | | | X | X | X |
| *Dasypus novemcinctus* | X | X | | | | |
| *Sciurus aureogaster* | X | X | X | | | |
| *Sciurus deppei* | X | X | X | | X | |
| *Heteromys desmarestianus* | X | X | X | X | X | |
| *Oryzomys alfaroi* | X | X | X | X | | |
| *Peromyscus mexicanus* | X | X | X | X | X | |
| *Dasyprocta mexicana* | X | | | | X | X |
| *Nasua nasua* | | X | | | | |
| *Potos flavus* | X | | | X | | X |
| *Procyon lotor* | | X | X | X | | |
| *Herpailurus yaguarondi* | X | X | | | | |

[1] Ba = *Brosimum alicastrum*, Fy = *Ficus yoponensis*, Am = *Astrocaryum mexicanum*, Na = *Nectandra ambigens*, Cb = *Cymbopetalum baillonii*, Oo = *Omphalea oleifera*.

Table 4. Number of spiny pocket mice *Heteromys desmarestianus* (Hd) and Mexican deermice *Peromyscus mexicanus* (Pm) live-trapped on plots after completion of the experiments. Mice were captured on mature forest for the density-dependent seed removal experiments, and gaps, mid-succession, and mature forest habitats, for the habitat-dependent seed removal experiments.

| | Density-dependent experiment | | | | Habitat-dependent experiment | | | |
|---|---|---|---|---|---|---|---|---|
| | Mature forest | | Gap | | Mid-succession | | Mature forest | |
| Plant species | Hd | Pm | Hd | Pm | Hd | Pm | Hd | Pm |
| *Omphalea oleifera* (May, 1986) | 1 | 3 | 1 | 2 | 2 | 2 | 1 | 1 |
| *Cymbopetalum baillonii* (Jun. 1986) | 7 | 5 | 2 | 3 | 3 | 3 | 5 | 5 |
| *Ficus yoponensis* (Oct. 1986) | 3 | 4 | 2 | 2 | 5 | 4 | 3 | 2 |
| *Astrocaryum mexicanum* (Dec. 1986) | 12 | 8 | 6 | 12 | 2 | 3 | 2 | 8 |
| *Nectandra ambigens* (Jan. 1987) | 12 | 13 | 6 | 10 | 10 | 10 | 5 | 11 |
| *Brosimum alicastrum* (Jul. 1987) | 6 | 8 | 1 | 2 | 1 | 3 | 3 | 3 |

1997), so postdispersal fruit and seed removal mainly resulted from small feeding choices of only forest-dwelling rodents for the tested plant species. Postdispersal fruit and seed removal varied more than five-fold for *N. ambigens*, *B. alicastrum*, *A. mexicanum* and *C. baillonii* fruits or seeds compared with *F. yoponensis* fruits, and *O. oleifera* seeds were not removed, supporting our predictions (Martínez-Gallardo & Sánchez-Cordero 1993). Field observations indicated that spiny pocket mice track fruit falls of plant species of high profitability. Population and reproductive peaks of spiny pocket mice at Los Tuxtlas match the overlapping fruit fall of *C. baillonii*, *B. alicastrum*, *N. ambigens* and *A. mexicanum*, and fruits and seeds of these species are frequently found in the cheek-pouches of wild-caught mice (Sánchez-Cordero 1993, Sánchez-Cordero & Fleming 1993).

Postdispersal fruit and seed removal was density-dependent for some plant species tested, with a one-third to a one-fold increase in removal values in high compared to low density *C. baillonii* seed patches and *A. mexicanum* fruit patches.

*Nectandra ambigens* showed the highest fruit removal due perhaps to a high density of mice when this experiment was conducted (Figures 1 & 2, Table 3). No density-dependent fruit removal was apparent for *B. alicastrum* and *F. yoponensis*.

Density-dependent removal may result from spiny pocket mice and Mexican deermice concentrating their foraging activity on high density fruit and seed patches of some plant species tested. These mice may be responding to a 'giving up density' (GUD) when foraging on these depletable food patches, as do several granivorous rodents in desert habitats (Brown & Mitchell 1989). Rich patches of some fruit and seed species tested may give off more sensory cues to these forest-dwelling rodents compared to poor patches, thus increasing the encounter rate. Massive fruit crops of *C. baillonii*, *B. alicastrum*, *N. ambigens* and *F. yoponensis* producing intensive fermented odours attracted other frugivorous mammals such as peccaries, pacas, and coatis even from long distances (Martínez-Gallardo & Sánchez-Cordero 1997). Likewise, low density patches may already be below the GUD, hence although detected, they are rejected by these small rodents. Mice may be also discouraged from revisiting known poor patches compared to rich patches of some plant species tested, particularly in habitats with high predatory risk (Brown *et al.* 1988). Density-dependent seed removal has been documented for several plant species in the Neotropics (Howe *et al.* 1985, Janzen 1971, Schupp 1988a).

Postdispersal fruit and seed removal was habitat-dependent for most plant species tested, with lower removal in gaps compared to mature forest for *N. ambigens*, *B. alicastrum* and *A. mexicanum* fruits and *C. baillonii* seeds (Figure 2). Spiny pocket mice and Mexican deermice at Los Tuxtlas concentrated their foraging activity on mid-succession or mature forest understorey, perhaps to avoid a higher predation risk on gaps imposed by owls like *Ciccaba virgata*, and snakes like vipers *Bothrops asper*, which appear to be abundant predators in this microhabitat (G. Pérez-Higareda, *pers. comm.*).

Although this study supports a habitat-dependent postdispersal fruit and seed removal hypothesis, our results differ somewhat with other studies in Neotropical lowland rain forests. Higher seed removal in gaps compared to the forest understorey for the subcanopy tree *Faramea occidentalis* (Rubiaceae) on Barro Colorado Island, Panama, and the palm *Welfia georgii* in La Selva, Costa Rica, has been attributed to a concentration of rodent foraging activity in gaps at both sites (Schupp 1988a,b; Schupp & Frost 1989). Foraging seed-eating rodents have been documented to discriminate among habitats in other geographical regions such as Costa Rican dry forests and North American temperate forest (Janzen 1986, Whelan *et al.* 1991).

Studies on postdispersal seed removal have documented the critical effects of terrestrial mammals on seed and seedling survival of several plant species in tropical rain forest communities (Smythe 1986, Sork 1987). High population levels of large terrestrial mammals on Barro Colorado Island compared to the mainland in Panama resulted in a lower seed and seedling survival for several abundant large-seeded tree species like *Gustavia superba* (Lecthidaceae), *Dipteryx panamensis* (Leguminosae) and *Faramea occidentalis* (Rubiaceae) (De Steven & Putz 1984, Sork 1987). Further, large terrestrial mammals such as cows and horses (surrogate Pleistocene megafauna; see Janzen & Martin 1982) introduced to pristine habitats, consume and disperse readily fruits and seed of the Guanacaste tree *Enterolobium cyclocarpum* (Leguminosae) (Janzen 1986).

Low abundance or local extinctions of large terrestrial frugivorous mammals due to overhunting or habitat reduction in tropical forests can change postdispersal removal of fruits and seeds for large-seeded plant species. Under these circumstances, postdispersal fruit and seed removal may instead be determined by the feeding choices of fewer, and perhaps more abundant terrestrial mammal species (De Steven & Putz 1984, Sork 1987). In Los Tuxtlas, small forest-dwelling rodents were the main terrestrial mammals responsible for removing fruits and seeds from the forest floor for the large-seeded tree and palm species tested. The contemporary defaunation may put small forest-dwelling rodents as the main postdispersal fruit and seed removal agents in this rain forest. It is likely that spiny pocket mice and Mexican deermice act as seed predators for the large-seeded tree and palm species tested. Caged mice consumed and readily destroyed fruits and seeds of preferred large-seeded plant species, or cache seeds in burrows below 30 cm, making successful seed germination highly unlikely (Martínez-Gallardo & Sánchez-Cordero 1993, 1997). This finding is particularly important in Los Tuxtlas since it holds the highest mouse density known (five-fold greater than recorded elsewhere) in Neotropical rainforests (Sánchez-Cordero 1993, Sánchez-Cordero & Fleming 1993).

If this hypothesis is true, then future forest composition at the Los Tuxtlas rain forest may be partially dominated by plant species with high seedling recruitment as determined by rodent food choice and avoidance, and/or rapid germination before mice detect seeds. Fruits and seeds containing deterrent or toxic compounds would have a higher seedling recruitment compared to those highly preferred and consumed by these small forest-dwelling rodents.

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