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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

A strong conditional mutualism limits and enhances seed dispersal and germination of a tropical palm

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Abstract Seed predation and seed dispersal can have strong effects on early life history stages of plants. These processes have often been studied as individual effects, but the degree to which their relative importance co-varies with seed predator abundance and how this influences seed germination rates is poorly understood. Therefore, we used a combination of observations and field experiments to determine the degree to which germination rates of the palm *Astrocaryum mexicanum* varied with abundance of a small mammal seed predator/disperser, *Heteromys desmarestianus*, in a lowland tropical forest. Patterns of abundance of the two species were strongly related; density of *H. desmarestianus* was low in sites with low density of *A. mexicanum* and vice versa. Rates of predation and dispersal of *A. mexicanum* seeds depended on abundance of *H. desmarestianus*; sites with high densities of *H. desmarestianus* had the highest rates of seed predation and lowest rates of seed germination, but a greater total number of seeds were dispersed and there was greater density of seedlings, saplings, and adults of *A. mexicanum* in these sites. When abundance of *H. desmarestianus* was experimentally reduced, rates of seed predation decreased, but so did dispersal of *A. mexicanum* seeds. Critically, rates of germination of dispersed seeds were 5 times greater than undispersed seeds. The results suggest that the relationship between *A. mexicanum* and *H. desmarestianus* is a conditional mutualism that results in a strong local effect on the abundance of each species. However, the magnitude and direction of these effects are determined by the relative strength of opposing, but related, mechanisms. *A. mexicanum* nuts provide *H. desmarestianus* with a critical food resource, and while seed predation on *A. mexicanum* nuts by *H. desmarestianus* is very intense, *A. mexicanum* ultimately benefits because of the relatively high germination rates of its seeds that are dispersed by *H. desmarestianus*.

Keywords Granivory · Predation limitation · Recruitment limitation · Seed predation

Introduction

Because of their contribution to recruitment limitation, seed dispersal and seed predation are considered two of the most significant processes that determine patterns of regeneration, diversity and spatial structuring in plant communities (Muller-Landau et al. 2002; Schupp et al. 2002). While it is evident that seed dispersal and seed predation have strong population- and community-level effects on plants, it is also becoming increasingly clear that their relative strength can vary widely (Howe and Miriti 2004). In some cases regeneration and spatial pattern of trees may be limited by high rates of seed predation (Silman et al. 2003; Kaufman and Maron 2006; Orrock et al. 2006), in others they may be

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limited by low rates of seed dispersal (Cordeiro and Howe 2003; Makana and Thomas 2004), while in some other cases spatial patterns appear to result from high rather than low rates of seed dispersal (Webb and Peart 2001).

There are several hypotheses on how recruitment is determined by where seeds are dispersed (Wenny 2001; Schupp et al. 2002). In contrast, hypotheses on the relationship between seed survival and the dynamics of seed predator populations are almost entirely ad hoc (but see Nathan and Casagrandi 2004; Adler and Muller-Landau 2005; Mari et al. 2008). In general, the degree to which seed predators influence seed survival will depend in large part on three factors: the species-specific ratio of seeds eaten or dispersed, variation in seed predator abundance, and the degree of overlap in diet in seed predator guilds. Many animal species exploit seeds and most can be considered both seed predators and dispersers, but there is great variability in the proportion of seeds different species disperse. In some cases animals disperse a high enough proportion of seeds of some plant species that the relationship is considered a mutualism (Longland et al. 2001), while in other cases animal species disperse few if any of the seeds they exploit (Beck 2006). Numerous studies have shown that changes in density of seed predator/disperser populations result in shifts in patterns of seed predation and dispersal (Adler and Kestell 1998; Curran and Leighton 2000; Wright et al. 2000; DeMattia et al. 2004), while the degree of diet overlap in seed predator/disperser guilds determines the overall intensity of seed predation and the extent of seed dispersal. In addition, interactions among these factors could have very different effects on plant distribution and abundance. For instance, changes in seed predator abundance may not necessarily influence distribution of a plant species but it could have a major influence on its abundance (Silman et al. 2003; DeMattia et al. 2004). Alternatively, if the seed predator/disperser guild was composed in large part of species that were primarily seed predators, changes in the composition of the guild could result in changes in both plant distribution and abundance (Kaufman and Maron 2006; Orrock et al. 2006).

In this study we examined the degree to which germination rates of the palm *Astrocaryum mexicanum* Liebm. Ex Mart. (Arecaceae) were determined by seed predation and seed dispersal, and whether the relative rates of seed predation and dispersal varied with alteration in species composition of the seed predator/disperser guild. In the course of previous investigations (Brewer and Rejmánek 1999; Brewer 2001; Klinger 2007; Klinger and Rejmánek 2009) we observed that a large proportion of *A. mexicanum* nuts were both preyed on and dispersed by the most abundant small mammal in the forest, *Heteromys desmarestianus* subsp. *desmarestianus* Gray (Heteromyidae). The spatial patterns of abundance of the two species co-varied and they seemed to have a reciprocal positive effect on each other (R. Klinger and M. Rejmánek, unpublished data). It was likely that *A. mexicanum* had a strong influence on the abundance of *H. desmarestianus* because of food availability, but how *H. desmarestianus* influenced abundance of *A. mexicanum* was less clear. The population dynamics of *H. desmarestianus* are driven primarily by food availability, with *A. mexicanum* nuts being their only year-round food resource (Klinger 2006, 2007). So, in sites where, or during periods when, food availability was high, abundance of *H. desmarestianus* was also high. But in these sites or during these periods when food availability was high predation on *A. mexicanum* nuts was also high (Klinger and Rejmánek 2009). Although seed predation by *H. desmarestianus* seemed to be a major influence on the spatial patterns of *A. mexicanum*, these patterns could have been due to seed dispersal by *H. desmarestianus*, high seed predation rates from other mammals, or because some sites were less suitable for germination and growth of *A. mexicanum* than others.

We hypothesized that seed predation and seed dispersal would have a much greater effect on germination rates of *A. mexicanum* seeds than abiotic conditions, and that germination rates would be consistently influenced more by seed predation by *H. desmarestianus* than seed dispersal. To test our hypotheses we compared rates of seed predation, seed dispersal, and germination among sites with varying abundance of *A. mexicanum*, including three sites where we used removal trapping to reduce the abundance of *H. desmarestianus*. This allowed us to directly evaluate whether experimental reduction of *H. desmarestianus* density in sites where density of *A. mexicanum* was high resulted in patterns of seed predation, seed dispersal and germination similar to sites where density of *A. mexicanum* was naturally low, and the degree to which seed predation and dispersal of *A. mexicanum* was compensated by other small mammal species after density of *H. desmarestianus* was reduced. We expected that: (1) reduction in abundance of *H. desmarestianus* would result in a significant decrease in seed predation and higher germination rates of *A. mexicanum* seeds, and (2) germination and initial establishment rates of *A. mexicanum* seeds would not vary among sites independently of density of *H. desmarestianus* or other mammal seed predators/dispersers.

Materials and methods

Study area and species

The study was conducted from January 2004 to March 2005 in a 5-km^2 section of the Bladen Nature Reserve (BNR), a 350-km^2 area located within the Maya Mountains in southern Belize (16°33′N, 88°43′W). The Bladen branch of the Monkey River runs through the BNR, with the floodplain widening into broad benches (flats) on the valley floor. Steep, rugged slopes surrounding the valley floor comprise the majority of the area. The fauna and flora remain entirely intact (Klinger 2006). The vegetation is composed primarily of evergreen tropical forest, with relatively high tree species diversity for the latitude (Brewer et al. 2003). The climate is seasonal, with the wet season occurring from June to January.

Heteromys desmarestianus and *Astrocaryum mexicanum* co-occur throughout northern Central America (Henderson et al. 1995; Reid 1997). *H. desmarestianus* (mean body mass = 87 g) is the most abundant small mammal in the BNR and plays significant roles as both seed predator and disperser (Brewer and Rejmánek 1999; Klinger 2006). *A. mexicanum* nuts (mean mass = 17 g; Brewer 2001) are a particularly important food source for *H. desmarestianus* throughout much of their range (Martinez-Gallardo and Sanchez-Cordero 1993; Brewer and Rejmánek 1999). *A. mexicanum* is the most abundant understory palm in the BNR (Brewer 2001).

Small mammal abundance and removal of *H. desmarestianus*

Mark-recapture trapping of small mammals was conducted at nine randomly located plots (“grids” hereafter); six 0.5-ha grids on the flats and three 1.0-ha grids on the slopes (mean slope angle = 38°). A pilot study conducted in 1999 indicated abundance of *H. desmarestianus* was relatively low on the slopes, therefore the larger grids were used to increase the number of small mammals that were captured. All nine grids were in primary forest with similar vegetation structure.

Distances between the grids on the flats ranged from 125 to 375 m. Trap stations consisting of a single Sherman live trap (model XLK; http://www.shermantraps.com) were set in a 10 × 10 array with 7-m spacing between stations. Three of the grids on the flats were randomly selected to be control grids (no removal of *H. desmarestianus*) and three as removal grids (removal of *H. desmarestianus* for 3 months; “DR grids” hereafter).

The grids on the slopes were arranged as a 5 × 20 array with 10-m spacing between trap stations. The rectangular arrangement was used on the slopes so that the trap lines covered the entire slope, extending from 10 m above the flats to the top of the ridge. Distances of the grids on the slopes from those on the flats were 135–450 m; distances between the grids on the slopes were 425–1,000 m.

Trapping on the flats was conducted for 5 consecutive days during each of eight periods: January 2004, February 2004, March 2004, April 2004, August 2004, October 2004, December 2004, and March 2005. Trapping on the slopes was conducted for 5 consecutive days in each of five periods; February 2004, May 2004, September 2004, December 2004, and March 2005.

The density of *H. desmarestianus* was reduced in the DR grids from 22 May to 12 August 2004. Trapping was done every other week until all *H. desmarestianus* were removed (2–5 days). *H. desmarestianus* removed from the grids were kept for feeding trials (see below). Trapping was not conducted in the control grids from May through July because of time constraints associated with the removal trapping. After 12 August density of *H. desmarestianus* in the DR grids was allowed to re-establish through natural immigration and reproduction.

Distribution and abundance of *A. mexicanum*

A count of the number of *A. mexicanum* adults, saplings and seedlings was done in January–February 2005 in 20 randomly selected plots within each grid. Plots were 49 m^2 (7 m × 7 m) in area on the flats and 100 m^2 (10 m × 10 m) on the slopes. Adults were classified as having a height ≥ 1 m or evidence of fruiting at least once, saplings as having a woody stem <1 m and no evidence of fruiting, and seedlings as not having a woody stem.

Seed removal

Seed-removal experiments were conducted once before (February–May 2004), once during (June–September 2004), and twice after (October–December 2004 and January–March 2005) removal of *H. desmarestianus* from the DR grids. Fifteen *A. mexicanum* nuts (“seeds” hereafter) were placed in each of nine randomly located 1-m^2 plots per grid. In previous studies we found that *A. mexicanum* seeds dessicate, rot, or become infested with bruchid beetle larvae within 2–3 months of primary dispersal (Brewer and Rejmánek 1999; Brewer 2001; Klinger 2007). Therefore, we counted the number of seeds that were removed from each plot at regular intervals for 90 days.

Consumption of *A. mexicanum* seeds

Three cameras connected to infrared motion sensors (TrailMaster model 1550) were moved among the seed plots to identify the mammal species removing the seeds. One camera/seed plot was set for 2–3 days then moved to another seed plot.

Controlled feeding experiments were used to determine consumption of *A. mexicanum* seeds by small rodents. Five *H. desmarestianus* from the DR grids and five adults of each of two murid rodent species, *Ototylomys phyllotis* Merriam and *Sigmodon hispidus* Say & Ord, were used in cafeteria-style feeding trials. *O. phyllotis* and *S. hispidus* are the only other commonly occurring rodents in the BNR (Klinger 2006) and were captured in arbitrary locations 1 km from the trapping grids.

Each individual was housed in a 16 cm × 5 cm × 5 cm wire cage and maintained with free water and from ten to 15 kernels of whole corn (*Zea mays*; 5–15 g total) and rolled oats (5–10 g total) provided ad libitum. The feeding trials consisted of removal of the maintenance diet and then providing each of the fifteen individuals with three *A. mexicanum* seeds (15–18 g each), as well as from ten to 12 whole peanuts (40–45 g total) and three slices of banana or plantain (15–20 g each). The trials were conducted 5 times in July and August 2004, with each trial separated by 3–4 days. The number of *A. mexicanum* seeds that were consumed was monitored each morning for 3 consecutive days. The peanuts and plantain were included in the trials because some species did not consume the *A. mexicanum* seeds and required supplemental food (see "Results"). Peanuts and plantain provided food different from that in the maintenance diet, thereby avoiding bias due to habituation to a particular diet but still enabling comparisons to be made among the three species. These protocols were consistent with guidelines and recommendations by the Animal Care and Use Committee at the University of California, Davis.

Seed germination

Seed-removal plots

A. mexicanum seeds that remained in the seed-removal plots were monitored for germination at weekly intervals for 90 days. At the end of each monitoring period the seeds were classified as germinated or dead.

Exclosures

Germination rates of *A. mexicanum* were estimated from December 2004–March 2005 in nine 4-m^2 (4 m × 1 m) plots. A single plot was located randomly within each grid. The plots were divided into two randomly selected sides; one enclosed by wire screening and the other left unscreened. The screen was buried to a depth of 4 cm to reduce the likelihood of small mammals entering the enclosure. One hundred *A. mexicanum* seeds were scattered in each enclosed and open part of the plots and checked for germination at weekly intervals for 90 days. At the end of the monitoring period the seeds were classified as germinated or dead.

Seed fate

Seed fate was estimated with a spool and thread method. One to six seeds were threaded with nylon carpet string, placed in the seed-removal or seed-germination plots, then checked every 3–5 days. Fate was classified as eaten (string only found), taken into a burrow, cached (surface or buried in leaf litter), or undetermined. Cached seeds were marked with a stake flag and monitored for 3 months. At the end of the monitoring period they were classified as germinated, dead, or missing.

Data analysis

Small mammal density

With the exception of the DR grids from May to September 2004, density estimates (individuals ha^{-1}) of *H. desmarestianus*, *Ototylomys phyllotis*, and *Sigmodon hispidus* were derived from the robust design model (Pollock et al. 1990) using program MARK (Cooch and White 2002). Details on model-selection procedures for the density estimates are given in Klinger (2007). Density of *H. desmarestianus* in the DR grids during the removal trapping period was based on a closed population removal trapping model (M_{hb}), using program CAPTURE (Otis et al. 1978; Rexstad and Burnham 1991). Ordinary least-squares regression was used to evaluate the assumption of a linear decline in the number of captures for the M_{hb} model. Paired *t*-tests were used to evaluate differences in density of *H. desmarestianus* between the flats and the lower slope ($\leq$30 m) and the flats and the mid and upper slopes (>30 m).

Non-linear regression was used to analyze the relationship between elevation above the flats and the distribution of the three small mammal species. The dependent variable was the number of unique individuals captured at each trap station (pooled across time periods). Recaptures of individuals at the same trap were not included to avoid non-independence. The data were fit by a simple exponential equation $e^{(a + b*elevation)}$, where e is the base of natural logarithms, e^a is the intercept, and b the slope parameter. Parameter estimates were obtained by least squares using the Gauss–Newton method and considered to be significant if their 95% confidence intervals did not include zero.

Distribution of A. mexicanum, seed removal, and seed germination rates

One-way multivariate nested ANOVA (MANOVA) was used to test for differences in density of *A. mexicanum* between sites (flats and slopes). The nested factor was plots within sites. Because the area of the plots differed between flats (0.005 ha) and slopes (0.01 ha), density was standardized as stems per 0.005 ha. The dependent variables were densities (log +1 transformed) of the age classes of *A. mexicanum*. Non-linear regression was used to analyze the relationship between elevation above the flats and the distribution of adult *A. mexicanum*. The relationship between elevation and distribution of *A. mexicanum* saplings and seedlings was not analyzed because of their low abundance on the slopes (see "Results").

The Kaplan–Meier estimator and log-rank tests (Kleinbaum 1996) were used to analyze differences in removal rates of *A. mexicanum* seeds between sites across the four seasons. Profile analysis (Tabachnik and Fidell 1996) was used to test for differences in the total proportion of *A. mexicanum* seeds removed between the sites across the four seasons. ANOVAs followed by planned comparisons were used to test the difference between sites in the total proportion (after angular transformation) of *A. mexicanum* seeds removed.

Generalized linear models (McCullagh and Nelder 1989) with a binomial error structure and logit-link were used to analyze differences in the proportion of *A. mexicanum* seeds: (1) removed from open and closed plots (exclosures) between sites (flats and slopes, and (2) that germinated in open and closed plots between sites. We corrected for extra-binomial error in both analyses, and evaluated significance of the regression coefficients with a z-test. Differences between regression coefficients were evaluated with Wald's test.

Multiway contingency tables (MCT; Christensen 1997) were used to analyze: (1) differences in the frequencies of undispersed *A. mexicanum* seeds from the seed-removal plots that germinated across sites and periods; (2) differences between sites in the frequencies of germinated *A. mexicanum* seeds that were either dispersed or undispersed; and (3) differences in fate for threaded seeds among sites and periods, with fate pooled into two categories: eaten (eaten + burrow) and cached (surface + buried). MCTs are used to analyze frequencies when there are more than two categorical response (germinated vs. ungerminated, eaten vs. cached) and predictor variables (dispersed vs. undispersed, site, time period). The significance of the individual and interactive effects of the variables is tested by removing each variable from the model and evaluating the reduction in fit relative to the full model (all variables included in the model). Reduction in model fit is evaluated by the difference in the likelihood-ratio χ^2-value between the full and reduced models (Christensen 1997). Because of small sample sizes, data on dispersed *A. mexicanum* seeds were pooled across time periods.

Results

Small mammal abundance and removal of *Heteromys desmarestianus*

Density of *H. desmarestianus* on the flats was 8–10 times greater than that of *Ototylomys phyllotis* or *Sigmodon hispidus* (Table 1). In general, density of *H. desmarestianus* was 4.5 times greater on the flats than on the slopes (Table 1). Removal trapping of *H. desmarestianus* between June 2004 and August 2004 resulted in a 90% decrease in their abundance relative to the control grids. Density of *H. desmarestianus* in the DR grids during this period was comparable to or less than its density on the slopes (Table 1).

Density of *O. phyllotis* was on average 4.5 times greater on the slopes than on the flats, while density of *S. hispidus* was 4–10 times greater on the flats than the slopes (Table 1). There was a significant decline in captures of *H. desmarestianus* and *S. hispidus* with increasing elevation ($r = -0.915$ and -0.704, respectively; Fig. 1). Mean density of *H. desmarestianus* (per hectare) on the flats (excluding the removal period) was 50.3 ± 1.4 SE and on the lower slopes 44.0 ± 4.9 SE ($t = 1.320$, $df = 4$, $P \leq 0.257$). Mean density of *H. desmarestianus* on the mid and upper slopes was 8.9 ± 1.2 SE, which was significantly lower than their density on the flats ($t = 9.053$, $df = 4$, $P \leq 0.001$). Captures of *O. phyllotis* increased significantly with increasing elevation ($r = 0.745$; Fig. 1). Eighty-four percent of the captures of *H. desmarestianus* occurred ≤100 m above the flats. No *S. hispidus* were captured >120 m above the flats. Sixty-seven percent of the captures of *O. phyllotis* occurred ≥100 m above the flats.

Distribution and abundance of *Astrocaryum mexicanum*

Densities of adult, sapling, and seedling *A. mexicanum* (stems 0.005 ha^{-1}) were significantly lower on the slopes than the flats ($P < 0.0001$; Electronic Appendix A). Seedling density was 14.00 (±1.84 SE) on the flats compared to 0.27 (±0.07 SE) on the slopes. Sapling density on the flats was 5.53 (±0.59 SE) and adult density 6.90 (±0.58 SE). Sapling density on the slopes was 0.15 (±0.05 SE) and adult density 1.03 (±0.15 SE). There was an inverse relationship between density of *A. mexicanum* adults and elevation ($r = -0.756$; Fig. 1). Seventy-six percent of *A. mexicanum* adults occurred below 100 m. Density of *H. desmarestianus* had a strong positive correlation with density of adult *A. mexicanum* (Fig. 2). More than 81% of the variation in mean density of *H. desmarestianus* was explained by variation in density of *A. mexicanum*.

Seed removal

Seed-removal plots

Removal rates and the total proportion of *A. mexicanum* seeds removed were significantly greater on the flats than the slopes in the three periods when density of *H. desmarestianus* was not manipulated ($P \leq 0.0001$; Fig. 3). The total proportion of *A. mexicanum* seeds removed was 31%

Table 1 Density estimates (individuals ha^{-1} ± SE) of three small mammal species at two sites [benches on the floodplain above the river (*Flats*), hillsides above the flats (*Slopes*)] in the Maya Mountains of southern Belize

Month/year	Density		
	Slopes	Control	Removal
Heteromys desmarestianus			
January 2004		25.6 ± 4.0	19.9 ± 1.8
February 2004	6.9 ± 0.4	36.4 ± 1.1	44.7 ± 1.0
March 2004		42.8 ± 0.8	40.0 ± 1.0
April 2004		43.8 ± 1.1	44.4 ± 1.0
May 2004	10.2 ± 0.5		45.0 ± 0.8
June 2004[a]			5.0 ± 0.3
July 2004[a]			5.6 ± 0.3
August 2004[a]		67.7 ± 2.6	5.0 ± 0.1
September 2004	14.5 ± 0.7		
October 2004		58.5 ± 1.2	71.0 ± 2.6
December 2004	14.1 ± 0.7	48.0 ± 1.0	62.1 ± 1.0
March 2005	20.1 ± 0.8	71.5 ± 1.8	82.7 ± 1.3
	Slopes		Flats
Ototylomys phyllotis			
January 2004			2.0 ± 0.0
February 2004	3.3 ± 0.0		4.0 ± 2.0
March 2004			3.5 ± 1.5
April 2004			3.5 ± 1.5
May 2004	7.2 ± 0.4		
June 2004			
July 2004			
August 2004			2.0 ± 0.0
September 2004	12.8 ± 0.5		
October 2004			3.5 ± 1.5
December 2004	15.3 ± 0.6		2.1 ± 0.3
March 2005	16.3 ± 0.6		2.0 ± 0.0
Sigmodon hispidus			
January 2004			8.0 ± 1.6
February 2004	1.0 ± 0.1		10.3 ± 1.9
March 2004			7.1 ± 1.8
April 2004			3.7 ± 0.1
May 2004	0		
June 2004			
July 2004			
August 2004			3.0 ± 0.9
September 2004	1.4 ± 0.1		
October 2004			9.5 ± 2.3
December 2004	1.3 ± 0.1		5.1 ± 0.2
March 2005	2.0 ± 0.1		8.0 ± 1.4

Control (no removal of *H. desmarestianus*) and removal plots (removal of *H. desmarestianus*) were on the flats

[a] Months when density of *H. desmarestianus* was reduced

greater on the flats than on the slopes. Mean time to removal on the flats ranged from 13 to 31 days, while on the slopes it ranged from 36 to 57 days. Excluding the DR grids from June to August 2004, the total proportion of *A. mexicanum* seeds removed on the flats was 0.93 (±0.03 SE). There was a significant decrease in removal of *A. mexicanum* seeds on the slopes with increasing elevation ($F_{3,104} = 15.43$, $P < 0.0001$). The total proportion of *A. mexicanum* seeds removed on the lower 50 m of the slope was 0.84 (±0.05 SE), compared to 0.57 (±0.05 SE) 51–150 m above the flats, and 0.25 (±0.07 SE) above 150 m.

Reduction in density of *H. desmarestianus* from June to August 2004 resulted in a 70% decrease in the total proportion of *A. mexicanum* seeds that were removed on the flats ($F_{6,6} = 11.69$, $P = 0.0040$; Electronic Appendix B). Removal rates were significantly lower in the DR grids than in the controls or on the slopes during this period ($P \leq 0.0001$; Fig. 3). Mean time to removal in the control grids was 28 days, whereas it was 143 days in the DR grids and 57 days on the slopes.

Exclosures

No *A. mexicanum* seeds were removed from within the exclosures. Almost all (98.8%) of the *A. mexicanum* seeds were removed from the open plots on the flats, compared to 22.7% on the slopes ($z = 8.12$, $df = 7$, $P < 0.0001$).

Consumption of *A. mexicanum* seeds

A total of 51 photographs (39 on the flats, 12 on the slopes) of *H. desmarestianus* removing *A. mexicanum* seeds were taken. There were no photographs of other small mammals removing seeds. There was no evidence (strings above rather than below ground vegetation, seeds taken up trees) of other mammals taking any *A. mexicanum* seeds.

All *A. mexicanum* seeds offered to *H. desmarestianus* during the feeding trials were eaten within 3 days. *O. phyllotis* and *S. hispidus* consumed none of the *A. mexicanum* seeds.

Seed germination

Seed-removal plots

Overall, 89 of 1,171 (7.3%) undispersed *A. mexicanum* seeds germinated from January 2004 up to and including March 2005 (Table 2). A total of 51 germinated on the slopes and 38 on the flats. There was no significant difference in the percentage that germinated across time periods ($\chi^2 = 8.39$, $df = 9$, $P \geq 0.495$) or in the percentage that germinated in the control, DR, and slope grids ($\chi^2 = 9.43$,

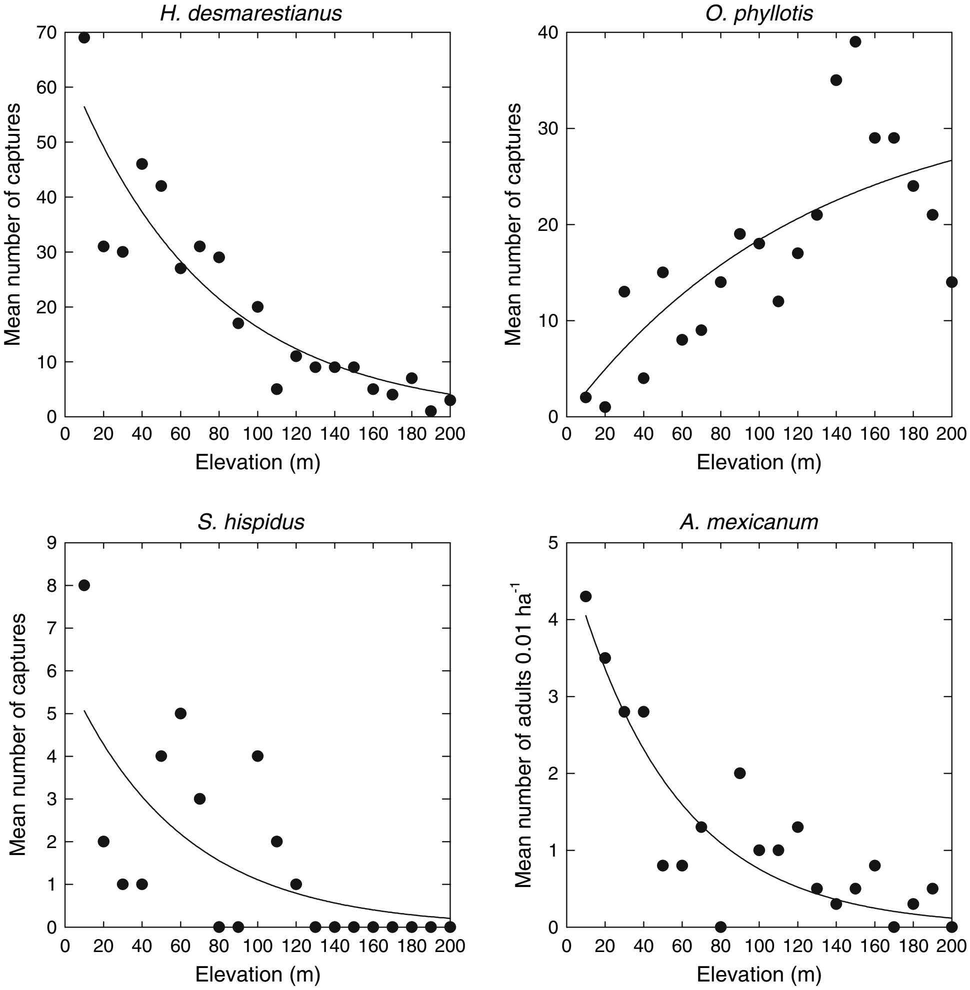

Fig. 1 The relationship between elevation and abundance of three small mammals (*Heteromys desmarestianus*, *Ototylomys phyllotis*, and *Sigmodon hispidus*) and the palm *Astrocaryum mexicanum* in the Bladen Nature Reserve (BNR), Belize. The slopes for all the regressions were considered significant (95% confidence intervals did not include zero)

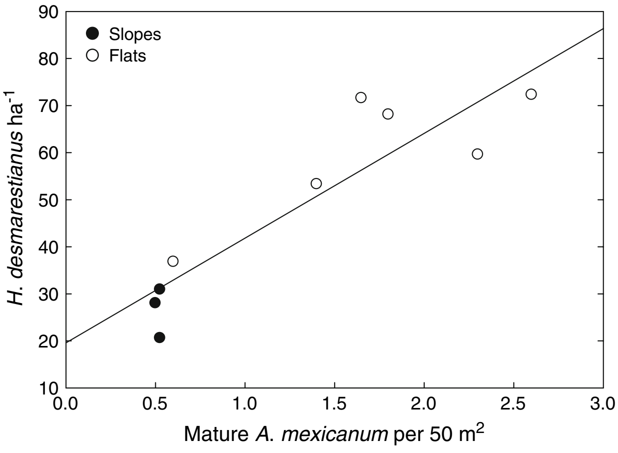

Fig. 2 The correlation between mean density of the small mammal *H. desmarestianus* and mean density of mature individuals of the palm *A. mexicanum* in nine plots in the BNR, Belize, January 2004 up to and including March 2005. *Flats* Plots located on the valley floor above the river, *Slopes* plots located on hillsides above the flats

df = 8, $P \geq 0.307$). Germination rates in the control plots ranged from 0 to 4.2%, from 0 to 10.6% in the removal grids, and from 4.8 to 8.4% on the slopes.

Threaded seeds

There was no significant difference in the percentage of dispersed seeds that germinated on the slopes and the flats (7 vs. 4%, respectively; $\chi^2 = 1.22$, $df = 1$, $P = 0.269$). However, the total number that germinated on the flats was almost 3 times greater than on the slopes ($n = 17$ vs. $n = 6$, respectively).

There was no significant difference in the percentage of *A. mexicanum* seeds that germinated across time periods when dispersed and undispersed seed data were combined ($\chi^2 = 7.67$, $df = 6$, $P \geq 0.264$). However, dispersed seeds were almost 5 times more likely to germinate than undispersed seeds ($\chi^2 = 42.75$, $df = 4$, $P < 0.0001$; Table 2).

Exclosures

Germination rates in closed and open plots varied between flats and slopes ($z = 3.407$, $P = 0.0003$). The germination rate of *A. mexicanum* seeds in enclosed plots on the slopes was 6.0 (±0.6 SE) while that in open plots on the slopes was 5.0 (±0.8 SE; $\chi^2 = 0.016$, $df = 1$, $P = 0.903$). In contrast,

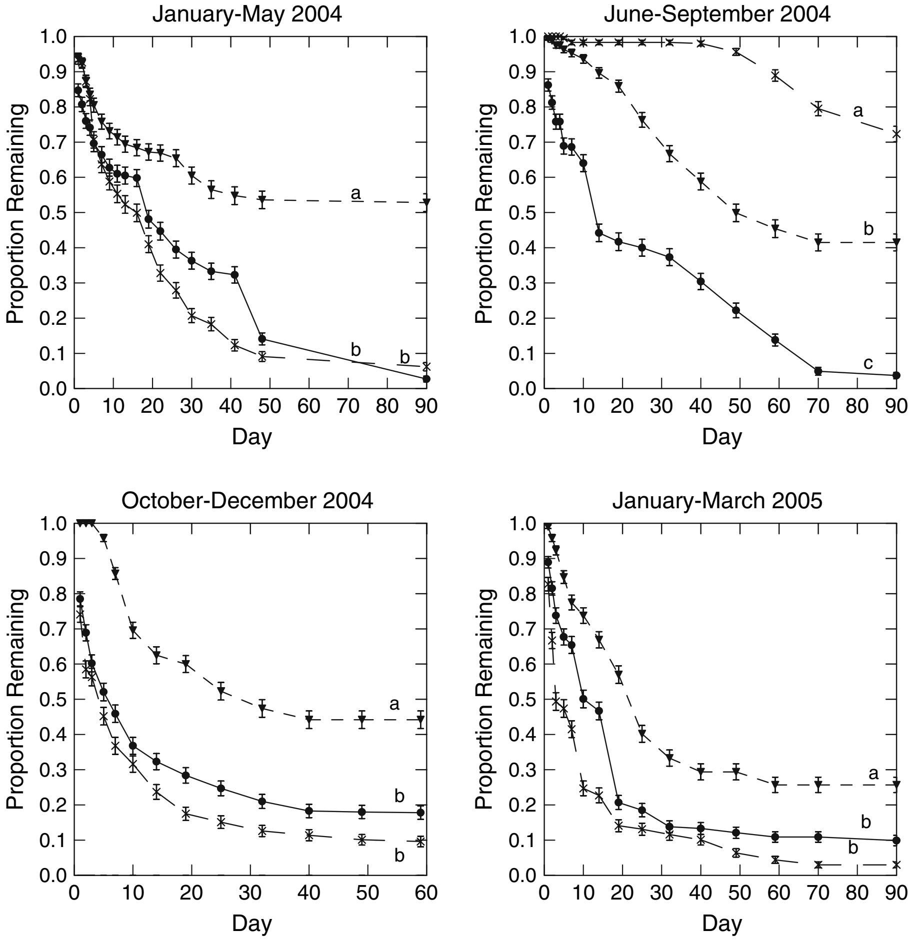

Fig. 3 The mean proportion (±SE) of *A. mexicanum* seeds remaining at three sites across four time periods in the BNR, Belize. The sites were: control plots (no removal of the small mammal *H. desmarestianus*; *solid lines*) on the flats (the valley floor above the river) in the BNR; removal plots on the flats of the BNR (removal of *H. desmarestianus* from June to August 2004; *long dashed lines*); plots on the slopes above the valley floor (low density of *H. desmarestianus*; *short dashed lines*). Removal of *H. desmarestianus* occurred over first 60 days in the June–September 2004 figure part. Proportions sharing the *same letter* are not significantly different ($P > 0.05$)

Table 2 The percentage of seeds of the palm *Astrocaryum mexicanum* that either died or germinated from January 2004 up to and including March 2005 in the Bladen Nature Reserve (BNR), Belize, on the flats and slopes, or when either dispersed or undispersed by the small mammal *H. desmarestianus*

Germination	Site			
	Flats		Slopes	
	Percentage	*N*	Percentage	*N*
Dead	92.5	468	92.3	614
Germinated	7.5	38	7.7	51
Total		506		665
Germination	**Dispersal**			
	Undispersed		Dispersed	
	Percentage	*N*	Percentage	*N*
Dead	92.4	1,082	64.6	42
Germinated	7.6	89	35.4	23
Total		1,171		65

germination rates on the flats were 5 times greater in the enclosed plots (5.2 ± 0.7 SE) than in the open plots (0.7 ± 0.01 SE; $\chi^2 = 20.722$, $df = 1$, $P < 0.0001$).

Seed fate

The fates of 496 threaded *A. mexicanum* seeds were determined during the study. Of this total, 65 (13.1%) were cached and the remainder either eaten or taken into a burrow. Excluding the period when the density of *H. desmarestianus* was reduced in the DR grids, the percentage of seeds on the flats that was eaten ranged from 81 to 97%, while the percentage eaten on the slopes ranged from 75 to 94% ($\chi^2 = 3.34$, $df = 4$, $P = 0.504$; Fig. 4). During the period when density of *H. desmarestianus* was reduced, the proportion of seeds eaten in the DR grids fell to 57% ($\chi^2 = 14.58$, $df = 6$, $P < 0.024$; Fig. 4).

Discussion

While many abiotic and biotic factors likely contribute to the regional distributions of *Heteromys desmarestianus* and *Astrocaryum mexicanum*, their mutual relationship as seed predator and food resource (Price and Jenkins 1986) clearly has a strong effect on the distribution and abundance patterns of each species in the BNR. *A. mexicanum* influences abundance of *H. desmarestianus* through food availability,

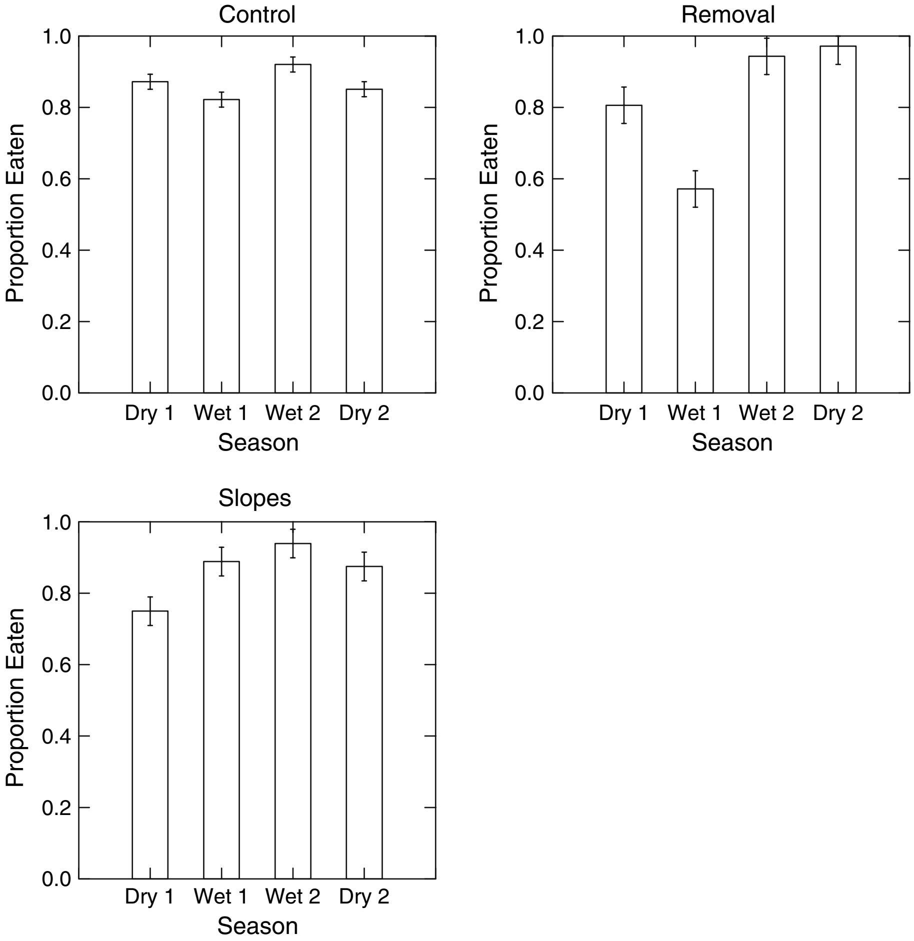

Fig. 4 The mean proportion (±SE) of threaded *A. mexicanum* seeds eaten at three sites across four time periods in the BNR, Belize. *Control* Plots with no removal of the small mammal *H. desmarestianus* on the flats (the valley floor above the river), *Removal* plots on the flats with removal of *H. desmarestianus* from June to August 2004); *Slopes* plots above the valley floor with a low density of *H. desmarestianus, Dry 1* January–May 2004, *Wet 1* June–September 2004, *Wet 2* October–December 2004, *Dry 2* January–March 2005

while *H. desmarestianus* influences germination rates of *A. mexicanum* seeds, and possibly abundance in later life history stages of the palm, through the interactive effects of seed predation and seed dispersal (Table 3).

Our hypothesis that germination rates of *A. mexicanum* seeds would be more strongly influenced by seed predation and dispersal than abiotic conditions was largely borne out. Many kinds of physical factors are known to influence palm density (Clark et al. 1995; Svenning 1999; Vormisto et al. 2004), and germination rates of *A. mexicanum* seeds would have varied independently of density of *H. desmarestianus* if abiotic conditions, especially those related to differences between slopes and flats (e.g. soil depth, soil texture, soil moisture capacity, nutrients), were a more important influence than biotic interactions. This was not the case though. When protected from removal by *H. desmarestianus*, germination rates of *A. mexicanum* seeds were similar on the flats and slopes. However, densities of *A. mexicanum* seedlings, saplings, and adults were an order of magnitude lower on the slopes than the flats, indicating that seed predation and dispersal were the dominant influences on germination of *A. mexicanum* seeds. This does not imply though that abiotic factors are not important for recruitment, because they may be exerting a strong influence on growth and survival rates of *A. mexicanum* seedlings and saplings.

Our hypothesis that seed predation would have a stronger influence than seed dispersal on germination rates of *A. mexicanum* seeds was not entirely supported. Germination rates on the flats were greater in enclosed than open plots and in the seed-removal plots when abundance of *H. desmarestianus* in the DR grids was reduced, which was consistent with our hypothesis. However, germination rates on the slopes were similar between enclosed and open plots and between the flats and slopes in the seed-removal plots, and the proportions of seeds eaten on the flats and slopes were similar. Critically, the number of seeds that were dispersed was dramatically lower in areas where density of *H. desmarestianus* was low, and dispersed seeds had much greater germination rates than undispersed seeds. This indicates that, in the BNR, the seed stage of *A. mexicanum's* life history is being strongly influenced by a complex interaction between density of *H. desmarestianus*, seed predation, and seed dispersal.

Low density of *H. desmarestianus* resulted in lower predation rates on *A. mexicanum* seeds, but this does not

Table 3 Summary statistics (mean ± SE) for nine variables related to the interactions between the small mammal seed predator/disperser *H. desmarestianus* and the palm *A. mexicanum* in the BNR, Belize, from January 2004 up to and including April 2005

Variable	Flats	Slopes	Removal
Heteromys density (ha^{-1})	50.3 (1.5)	13.2 (0.6)	5.2 (0.2)
Astrocaryum density (mature ha^{-1})	345.0 (28.9)	103.3 (14.8)	420.1 (44.5)
Astrocaryum density (saplings ha^{-1})	276.7 (29.7)	15 (4.6)	176.7 (29.3)
Astrocaryum density (seedlings ha^{-1})	700.0 (91.8)	26.7 (7.1)	663.3 (125.3)
Seed dispersal rate (%)	92.4 (2.0)	59.0 (3.7)	27.7 (6.8)
Seed predation rate (%)	86.6 (2.1)	86.3 (4.0)	57.1 (3.7)
Germination rate undispersed seeds (%)	2.4 (1.3)	7.6 (0.9)	10.6 (2.2)
Germination rate dispersed seeds (%)	3.9 (0.8)	7.3 (3.6)	
Total number of seeds germinating	17	6	

Statistics for the flats include control ($n = 3$) and removal ($n = 3$) plots on the floodplain exclusive of the period May–July 2004. Statistics for the removal plots are for the period May–July 2004 when trapping was used to reduce density of *H. desmarestianus* by 90%. Statistics for the slopes are for plots ($n = 3$) located on the hillsides above the floodplain. Empty cells in the removal column indicate that too few tagged seeds were dispersed ($n = 7$, none germinating) to derive meaningful estimates of germination during this period

necessarily mean there is a negative relationship between germination of *A. mexicanum* and abundance of *H. desmarestianus*. In sites where abundance of *H. desmarestianus* was high, germination rates of *A. mexicanum* seeds were limited by high rates of seed predation, but where abundance of *H. desmarestianus* was low, germination was limited by low rates of seed dispersal. Predation appears to largely be a compensatory source of mortality for *A. mexicanum* seeds, and the local distribution pattern of *A. mexicanum* benefits considerably from the seeds that are dispersed and buried by *H. desmarestianus*. Dispersed and buried seeds in tropical forests often have higher survival rates than those not dispersed or buried, primarily because of less predation by both vertebrates and invertebrates (Smythe 1989; Forget et al. 1998; Brewer and Webb 2001). However, while it is known that high seed predation or low rates of dispersal may limit abundance of plants (Webb and Peart 2001; Orrock et al. 2006), the simultaneous importance of each mechanism and how they may be directly contingent on seed predator/disperser abundance has not previously been reported. Although reduced germination rates do not necessarily mean seed predation and dispersal are limiting recruitment of *A. mexicanum*, each mechanism is contributing to reduced transition rates of seeds to seedlings in the BNR.

There are indications that the distribution of *A. mexicanum* in the BNR is influenced as much or more by the number than the proportion of seeds that are dispersed. *H. desmarestianus* consumed approximately the same proportion of *A. mexicanum* seeds on the flats as on the slopes, but the number of seeds that were dispersed on the flats was greater than on the slopes. In addition, despite high seed predation on the flats and similar germination rates among the flats and slopes, seedling density of *A. mexicanum* on the flats was considerably higher than on the upper slopes. This suggests a parallel between seed dispersal and predator–prey interactions; in many instances it may be critical to determine if germination depends on the number of seeds that are dispersed or the ratio relative to seed predator abundance (Abrams and Ginzburg 2000).

Mutualisms between plants and seed dispersers in the tropics are generally considered to be highly diffuse and coevolution rare (Herrera 1985). However, relatively specific facultative mutualisms can develop over more limited time and spatial scales and have a significant influence on distribution and abundance patterns of the species involved in the relationship (Bronstein 1994; Theimer 2005). Hulme (2002) hypothesized that granivores would likely act as mutualists under three conditions: when the plant depends on animals to disperse their seeds, when seeds are scatterhoarded rather than larderhoarded, and when resources are scarce. The relationship between *H. desmarestianus* and *A. mexicanum* clearly met two of these three criteria: seeds of *A. mexicanum* are dispersed exclusively by mammals, and while *H. desmarestianus* does larderhoard, scatterhoarding is also quite common. The relationship between caching rates and food availability was less clear. The overall high availability of food throughout most of this study limited the extent we could evaluate this relationship, but it is suggestive that caching rates of *A. mexicanum* in the BNR were twice as high in the year after a hurricane (October 2001) when overall food resources were very low (Klinger and Rejmánek 2009). However, densities of *H. desmarestianus* were also very low during this period (Klinger 2007). The strong relationship between *H. desmarestianus* and *A. mexicanum* in the BNR existed prior to the hurricane (Brewer and Rejmánek 1999), so it is unlikely our observations were artifacts of this major disturbance. The variation in caching rates in the year after the hurricane and when we conducted this study (3 years post-hurricane) raises the possibility though that it is not just resource scarcity but the per capita amount of food available to seed predators/dispersers that influences the formation of mutualisms (Theimer 2005).

The relationship between *H. desmarestianus* and *A. mexicanum* in the BNR would appear to be an example of what are typically considered diffuse interactions between palms and their seed predator/disperser species (Zona and

Henderson 1989). The seeds of *A. mexicanum* can, potentially, be handled by many other mammal species, and while *H. desmarestianus* consumes a wide variety of seeds (Klinger and Rejmánek 2009) it is clearly the only mammal in the BNR that consumes or disperses *A. mexicanum* seeds to any meaningful degree. Such specificity in a plant-seed disperser relationship is generally thought to be relatively uncommon; plant seeds are typically dispersed by multiple animal species and animals usually consume and disperse seeds of many plants (Wheelwright and Orians 1982). But plant–seed disperser relationships that are evolutionarily diffuse may still be specific enough at smaller spatial and temporal scales to have significant effects on density and distribution of both the plant and disperser species.

Reducing density of *H. desmarestianus* allowed a direct evaluation of the degree to which their seed dispersal benefited *A. mexicanum*. Reducing density of *A. mexicanum* seeds would have allowed a direct evaluation of the degree to which they benefited *H. desmarestianus*, but this was logistically impractical to do. However, there is abundant evidence of the importance of this part of the mutualism. Population dynamics and demography of mammals in the tropics are often related to bottom-up effects (Adler and Beatty 1997; Klinger 2006, 2007), and *A. mexicanum* seeds are clearly a very important food resource for *H. desmarestianus*. Survival rates of subadult *H. desmarestianus* are positively related to abundance of *A. mexicanum* seeds (Klinger 2007), and density of *H. desmarestianus* is greater in areas with greater abundance of *A. mexicanum* seeds. Because it is their only year-round food source and influences transition rates of subadults to adults, availability of *A. mexicanum* seeds likely sets a lower threshold of density for *H. desmarestianus*. This explains in large part why density of *H. desmarestianus* was lower on the slopes than the flats. More generally, it suggests that when seed disperser mutualisms are tightly coupled then the interaction may act as a feedback system determining distribution and abundance of each species. Studies of mutualisms in other systems have often focused on one pathway in the interaction while assuming that the pathway in the opposite direction was also important (Longland et al. 2001). Even though these assumptions may be correct, simply assuming so does not allow an evaluation of how strong the mutualism truly is.

Logistic constraints (trap availability, topography, and time) required us to have lower densities of traps and seed plots on the slopes than on the flats. However, differences in trap and seed plot densities likely had small or negligible effects on density estimates and seed-removal rates because their influence was minimal relative to home range size and density of *H. desmarestianus*. The minimum home range size for *H. desmarestianus* is approximately 100 m^2 (Fleming 1974), and their density and seed-removal rates on the lower slopes were comparable to those on the flats.

Because our study was restricted to the BNR our inferences must be limited to this particular forest. The densities of *H. desmarestianus* and *A. mexicanum* in the BNR are very similar to those reported from other forests in the northern Neotropics (Martinez-Ramos 1997; Martinez-Gallardo and Sanchez-Cordero 1997), but the reserve differs in some important respects from many other forests in Central America. The BNR has a high level of protection and is surrounded by a national park, a wildlife sanctuary, and several forest reserves. Consequently, illegal activities have been relatively localized and largely near the boundaries of the reserve. This is in contrast to many other protected areas in the Neotropics, which frequently exist as habitat islands with high levels of illegal activities, altered forest structure, and a depauperate fauna (Dirzo and Garcia 1992; Wright et al. 2000). Differences in species composition of the fauna and flora in these forests, either because of natural or anthropogenic factors, could result in very different interactions than we observed in the BNR. Despite this, we suspect that strong local plant-seed disperser mutualisms are more common than thought (Gove et al. 2007). However, we also expect that these mutualisms are restricted spatially and do not persist for long periods of time. Interaction strengths and direction may shift, and possibly quite rapidly, due to changing environmental conditions (Ovadia and Schmitz 2004) or anthropogenic influences (Wright et al. 2007). Nevertheless, even though they may be relatively localized both spatially and temporally, these conditional mutualisms likely leave a disproportionately strong historic imprint on the population structure and distribution of long-lived plant species.

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