

Predation and dispersal of large and small seeds of a tropical palm

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Seed size may vary greatly among individuals within plant species. What effects the extremes of this variation have for seeds taken by small mammals are poorly understood. Not all seeds removed by small mammals are necessarily eaten. Small rodents are common seed predators, but they may disperse a significant proportion of seeds by scatter hoarding them via burial. Size-dependent predation and dispersal of seeds has not been directly tested within a plant species for tropical rodents. This study tested whether or not large and small nuts of *Astrocaryum mexicanum* (Palmae) differed in their fates due to handling by the spiny pocket mouse *Heteromys desmarestianus* (Heteromyidae). Exclosures were used to give small rodents exclusive access to *A. mexicanum* nuts. *H. desmarestianus* preferentially consumed large over small *A. mexicanum* nuts, but cached (in burrows and by scatter hoarding) similar proportions of these nuts by size. Small nuts tended to be buried farther away from exclosures than large nuts. Although sample sizes of buried nuts were small, the rodents retrieved all buried large nuts, but 30% of the small nuts remained buried long enough to germinate. I also examined predispersal predation by insects and found that insects appear to have no size preference for *A. mexicanum* nuts, but insect predation appears to hinder nut development. Thus, nuts attacked by insects develop to be significantly smaller, with a low proportion of undamaged endosperm, than uninfested nuts. It is hypothesized that the preferential predation of large *A. mexicanum* nuts by *H. desmarestianus* is a response by these rodents to insect predation.

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From the minute progeny of the Orchidaceae to the 20-kg double coconut (*Lodoicea maldivica*, Palmae), the great range in seed size among plant taxa has been well documented (e.g. Ridley 1930, Harper et al. 1970, Westoby et al. 1992). The consequences of this variation for seed predators and dispersers is not well understood. All else being equal, larger seeds should experience greater predation than smaller seeds (Janzen 1969, 1971, Harper 1977), since larger food items often maximize energetic returns for foragers (e.g. see review by Schoener 1971). When encountering seeds of multiple plant taxa, however, seed predators are faced with food items that differ in more ways than by size alone;

nitrogen content, seed-coat thickness, and chemical defenses also vary substantially among plant taxa (Janzen 1969, 1971, Harper et al. 1970). For example, Blate et al. (1998) found that a negative association between seed size and predation rates might be due to other characters associated with seed size. Therefore, seed size may be a relatively less important character to predators faced with seed resources that vary in more ways than size.

Perhaps seed size is relatively important, however, to predators and dispersers of seeds within plant taxa. Although seed size variation within many plant taxa appears to be tightly constrained (e.g. Harper et al.

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1970, Harper 1977), a growing body of evidence suggests that seed size variation within plant taxa can be substantial (e.g. Janzen 1978, Howe and Richter 1982, Dirzo and Dominguez 1986, Manasse 1990). This variation may have significant implications for plant populations as well as for the animals that handle seeds. For example, increased seed size is associated with shorter dispersal distances (e.g. Howe and Schupp 1985, Hegde et al. 1991), fewer seeds per individual (e.g. Harper et al. 1970, Willson 1983, Westoby et al. 1992, Jakobsson and Eriksson 2000), better competitive ability of seedlings (e.g. Black 1958, Harper 1977, Stanton 1985, Bazzaz et al. 1989, Turnbull et al. 1999), and variation in nutrient content and allocation to protective tissues (e.g. Grubb and Burslem 1998). Despite this evidence, few studies have directly addressed how intraspecific seed size variation affects seed predation and dispersal in the field (Hare 1980, Ernst et al. 1989, Podolsky and Price 1990, Moegenburg 1996). Furthermore, animals may act as both predators and dispersers of seeds (e.g. Ridley 1930, Janzen 1971), but studies of seed predation often assume removal to be equivalent to predation – an assumption that is not necessarily valid, especially for rodents (e.g. Vander Wall and Smith 1987, Forget 1990, Vander Wall 1990, 1994, Brewer and Rejmánek 1999). Small rodents are among the most abundant terrestrial mammals in many communities, including tropical forests (Eisenberg 1980, Robinson and Redford 1986, Reid 1997), where they may play a significant role in determining the fates of seeds (Brewer and Rejmánek 1999).

I am unaware of any study in the tropics that has directly tested whether mammals discriminate among seeds of a single species based on seed size. The objective of this study was to investigate the fates of seeds of contrasting sizes within a tree species in a lowland tropical forest. Rather than attempt to follow seeds representing the entire spectrum of size variation that may exist within a species, this study compared how small rodents handled seeds that were of two clearly different size categories. Therefore, this was an analysis of the survival and fates of seeds in the tails of a relatively broad mean-size distribution of seeds represented by individuals of *Astrocaryum mexicanum*, a ubiquitous palm in northern Central America. *A. mexicanum* “seeds” (actually a type of nut, see below) are highly suitable for this type of experiment because they are variable in size and are attractive to the spiny pocket mouse, *Heteromys desmarestianus*. Removal of *A. mexicanum* seeds by this rodent has been shown to be rapid in the laboratory (Martínez-Gallardo and Sánchez-Cordero 1993) and in the field (Sánchez-Cordero and Martínez-Gallardo 1998, Brewer and Rejmánek 1999).

Methods

Study species and site

This study was conducted in the northeastern Bladen Nature Reserve (“BNR”; 16°33'N, 88°43'W; ca 45 m elevation) in the Maya Mountains, Belize. The study area is located in a lowland, evergreen seasonal tropical forest (Beard 1944) on alluvium over limestone. Annual rainfall in the area is approximately 2500–3000 mm, with a pronounced dry season from March through May. Most of the forests of the BNR, including the study area, are hunted but not logged.

The monoecious palm *Astrocaryum mexicanum* Liebm. ex Mart. is the most abundant tree in the study area (550 adults/ha), and is abundant in lowland wet forests from southern Mexico to northern Nicaragua (Henderson et al. 1995). Reproduction and demography of this palm have been well described in the literature (e.g. Sarukhán 1978, Piñero and Sarukhán 1982, Eguiarte et al. 1993). Fruiting individuals of *A. mexicanum* can be found throughout the year, but mature nuts are most abundant during the mid- to late wet season (September–November) and least abundant during the dry season. Infructescences are born and mature sequentially on each tree. The nuts are born together in tight clusters of about 25 nuts per infructescence.

The *A. mexicanum* nut (technically a nuculanum, Spjut 1994) is the smallest unit of dispersal (i.e. diaspore), and in that sense is equivalent to a seed, since it is the nut that is moved to a site (e.g. to a burrow or to cover on the forest floor) where it is peeled, or left intact. The nuts are obovoid, or top-shaped, and the thick and fibrous pericarp is densely covered with small spines (Fig. 1). Peeling of the nut by mammals damages the endosperm, which then rots, desiccates, and/or is consumed by insects when left unprotected (Brewer pers. obs.). Similar to a coconut, the immature *A. mexicanum* nut is at first filled with clear liquid and gelatinous endosperm that later be-

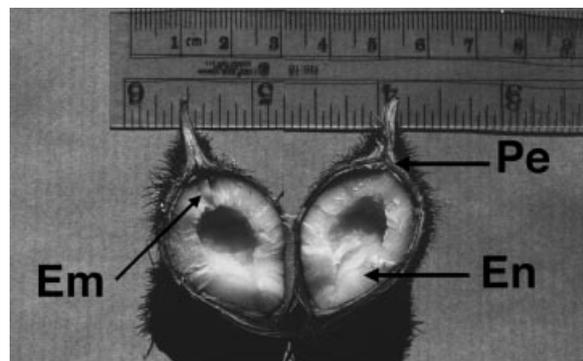


Fig. 1. An opened nut of *Astrocaryum mexicanum* showing the embryo (Em), pericarp with spines (Pe), and solid endosperm (En).

comes solid and white after the rest of the nut has been fully formed (Fig. 1). During the wet season, germination of mature nuts takes from 3 to 6 months (Brewer unpubl.).

Primary dispersal of mature *A. mexicanum* nuts is by gravity. Soon afterwards, the nuts are consumed beneath the palm by a wide variety of mammals, including small and large rodents and larger mammals such as peccaries (*Tayassu* spp.) (pers. obs.). The spiny pocket mouse *Heteromys desmarestianus*, however, is the dominant handler of *A. mexicanum* nuts in the study area (Brewer and Rejmánek 1999). More than 99% of the individual small mammals captured in traps baited with *A. mexicanum* nuts at the study site over two years were *H. desmarestianus* (Brewer and Rejmánek 1999, Brewer and Webb unpubl.). *H. desmarestianus* is a burrowing mouse that is also the most abundant terrestrial mammal in the study area (Brewer and Rejmánek 1999). It is often the most abundant terrestrial mammal in many of the forests where it is found throughout Central America (Reid 1997). Spiny pocket mice (including *Heteromys* spp. and *Liomys* spp.) have fur-lined, external cheek pouches, high energetic requirements, and actively forage for seeds ranging among species from 0.6 cm to 15+ cm long (Fleming 1977, Janzen 1982, Sánchez-Cordero and Fleming 1993, Brewer and Rejmánek 1999).

Size categories

Seed and nut measurements were taken from randomly selected *A. mexicanum* trees under closed canopy. Total nut length was measured with calipers, and nuts were subsampled for measurements of nut and seed mass, and seed length. Only fresh mass was measured, since suitable drying facilities were not available. The seeds have dense seed coats, however, and do not readily desiccate under the high-humidity conditions of the field site. In 1997, length and maximum diameter were measured for 1062 nuts from 45 randomly chosen trees ≥ 200 m away from the experimental site. Status of the seed – intact or damaged by insects – was also recorded by cutting open and examining each nut. Approximately 10–20% of nuts abort very early in development. These nuts rot during infructescence development and were not included in the experiment or analyses of nut attributes.

In order to compare removal rates and fates of nuts of different size, experimental nuts were divided into two size classes: “large” ≥ 58 mm long and “small” ≤ 41 mm long. Nut length was used in determining the categories, since it is the least ambiguous dimension, is the most easily measured character in the field, and because it is significantly correlated with other nut and seed size-based characters (Table 1). Large and small nuts were also collected for destructive measurements

Table 1. Nut and seed characteristics correlated with length of *Astrocaryum mexicanum* nuts.

Characteristic	<i>r</i> *	<i>n</i> fruits	<i>n</i> trees
Nut diameter (mm)	0.480	730	30
Nut mass (g)	0.754	673	40
Seed length (mm)	0.840	433	25
Seed diameter (mm)	0.242	80	25
Seed mass (g)	0.642	433	25

* $P < 0.0001$ for all correlations.

of nut, seed and embryo dimensions, and mass (Table 2).

Nut removal and fate

Small rodents were given exclusive access to the nuts of *A. mexicanum* in the removal and fate experiment from late September through October 1997. Large and small nuts were placed 20 cm apart in a 4×4 grid of alternating nut size inside 20 exclosures located ca 15–20 m apart in the study area (8 nuts size⁻¹ exclosure⁻¹; total $n = 160$ nuts per size class). Based on trapping studies and observations of seeds moved by *H. desmarestianus* (Brewer unpubl.), inter-trap and foraging distances of this small rodent are typically ≤ 15 m. Furthermore, seeds from any two exclosures in this experiment were never found together in one burrow or feeding place. Therefore, the exclosures may be considered to be independent. The $2 \text{ m} \times 2 \text{ m} \times 1 \text{ m}$ tall exclosures were constructed of hardware cloth (0.6-cm mesh) supported on the sides and corners by PVC-pipe stakes. At the base of each side, seven $6 \text{ cm} \times 7 \text{ cm}$ openings allowed access to the nuts by small rodents. The tops of the exclosures were open, but arboreal and scansorial mam-

Table 2. Characteristics of nuts from two size categories used for the *Astrocaryum mexicanum* removal experiment (mean \pm SE). “Large” ≥ 58 mm length and “small” ≤ 41 mm length.

Characteristic	Size category	
	Large	Small
Experimental nuts ($n_{\text{Large}} = 160$, $n_{\text{Small}} = 160$)		
Length (mm)	62.7 ± 0.0242	37.9 ± 0.0191
Independent random sample of nuts ($n_{\text{Large}} = 65$, $n_{\text{Small}} = 65$)		
Nut length (mm)	60.8 ± 0.38	36.2 ± 0.43
Nut mass (g)	14.3 ± 0.41	5.8 ± 0.27
Proportion of total mass as pericarp	0.55 ± 0.012	0.48 ± 0.016
Seed length (mm)	41.3 ± 0.36	25.3 ± 0.40
Seed mass (g)	7.0 ± 0.16	3.4 ± 0.14
Embryo length (mm)	3.8 ± 0.069	3.5 ± 0.080
Embryo mass (g)	0.012 ± 0.00047	0.0095 ± 0.00051

Nut characteristics are significantly different between size categories (*t*-test: all $P < 0.0001$, except for pericarp mass $P = 0.0002$, and embryo length $P = 0.003$).

imals do not remove nuts from these exclosures (Brewer and Rejmánek 1999).

The nuts were tagged such that their fates could be followed when they were removed, a method modified after Forget (1990; see also Brewer and Rejmánek 1999). The nuts were threaded through the apical pericarp with 2 mm × 150 cm pieces of white Dacron line tags (Izorline, Gardena, California). Each tag had a unique code of permanent ink marks indicating size category, exclosure replicate number, and replicate within exclosure. The tags are relatively light (1.0 g, cf. 45–120 g body weight of *H. desmarestianus*), are not tethered at an end, and do not appear to hamper movement of the nuts, as the tags have a somewhat slick surface, do not catch on objects, and only rarely wrap around debris or vegetation on the forest floor. Tagging does not affect removal rates or overall removal of these nuts (Brewer and Rejmánek 1999). Monitoring for nut removal and searches for removed seeds were conducted daily. Distance moved and fate were recorded for each nut removed from the exclosures. Careful searches up to 25 m radius were conducted for nuts removed from the experimental nut source, resulting in greater than 70% recovery rate by the author. Missing nuts were likely taken into burrows (see below). The tags can be seen even when the nuts are taken into underground burrows, although many tags are pulled completely into the burrow within 2 d (see Fig. 1 in Brewer and Rejmánek 1999).

Nuts removed from an exclosure could have one of four fates. They could be: (1) moved and taken to cover on the surface of the forest floor (“surface”; e.g. hollow leaf sheaths of *Attalea cohume*, piles of dead branches, etc.), (2) moved and scatter hoarded by shallow burial (“buried”), (3) taken underground into burrows (“burrows”), or (4) “missing” (i.e. deep into burrows, or possibly > 25 m away). All nuts not buried were considered to be killed because when they were taken from exclosures, they were either consumed on the spot, were peeled and therefore assumed to be dead (peeled seeds left by rodents desiccate, rot or are eaten by insects), or were taken to places (deep burrows, logs, palm leaf sheaths, etc.) where they die or do not survive as seedlings (Brewer pers. obs. and unpubl.). During a pilot experiment on seed dispersal and excavations of the burrows of *H. desmarestianus*, those nuts that were “missing” were found to be taken deep into burrows and the tags pulled in before they could be observed (25% of 125 removed seeds, $n = 6$ burrows).

Data analyses

All statistical tests were conducted using the Statview (Abacus Concepts 1996) and (SAS Institute 1990) statistical software. Relationships between seed and nut measurements and between nut number and length

were analyzed using simple linear regression. Means between nut categories with respect to mass and length were compared using *t*-tests.

Removal rates of small and large nuts were compared using nonparametric survival analysis. This type of analysis has the advantages of accommodating right-censored data (e.g. nuts still in exclosures at the end of the study but having unknown total survival times) and/or other data (e.g. nut survival times) that are not normally distributed (e.g. Muenchow 1986, Le 1997). Three functions were computed for this experiment. First, the survival function [$S(t)$], or survival rate, is the probability that a nut survives longer than time t . Second, the hazard, or risk, function [$\lambda(t)$] is a measure of interval-specific mortality, given survival until time t . The hazard function essentially measures the “prone-ness to failure” (Le 1997) as a function of the length of time the nut is in the exclosure. Third, the cumulative hazard plot shows how the hazard function changes over time. The survival functions were estimated using the Kaplan-Meier (or product-limit) method, and the actuarial method was used for estimating the hazard functions (Abacus Concepts 1996).

Log-rank (“Mantel-Cox”) and Breslow-Gehan-Wilcoxon tests were used to compare the survival functions between large and small nuts, after the survival data had been stratified by exclosure in order to remove exclosure effects. The log-rank test is more powerful in detecting differences in the tail of the survival curve (later survival), while the Breslow-Gehan-Wilcoxon test is more powerful in detecting differences in early survival (Abacus Concepts 1996, Kleinbaum 1996, Le 1997). Final survivals of large and small nuts were compared using contingency-table analysis.

Multivariate analysis of variance (MANOVA) was conducted on the effect of nut size on the proportions of nuts removed for each of the four fate categories (to cover on the soil surface, buried/scatter hoarded, taken into burrows, or missing). Proportions of nuts per exclosure in each fate category were angular-transformed in order to meet the assumptions of the analysis.

Repeated measures analyses of variance were conducted, using SAS, on the effect of nut size on the per-exclosure mean distance of nuts removed. Fates of the seeds were treated as the repeated measure. The univariate approach was used because not all of the experimental units were present in the analysis. For example, some exclosures had nuts that were only taken to burrows; thus replicates for the buried and surface fates were missing. Differences between sizes in the mean distances moved, within fates, were also compared separately using paired *t*-tests; distances of seeds of each size moved from any one exclosure could not be assumed to be independent for certain fates. For example, the distances that nuts could be moved to burrows was constrained by the limited number of burrows, or

places where cover could be used, that exist in any one area of forest. Any effect of rodents on the distances of nuts that were buried – the fate of primary interest – might be masked in an ANOVA by the high number of replicates of the constrained fates in an analysis of variance. Furthermore, separate (by fate category) analysis of the distances that nuts were moved is not unrealistic, since rodents move nuts of *A. mexicanum* in separate trips away from the enclosure (Brewer pers. obs.).

Results

Nut characteristics

Mean size of undamaged nuts varies considerably among individual trees (for 45 trees: mean length = 29 mm to 63 mm, $n = 8\text{--}34$ nuts per infructescence/tree; mean weight = 7 g to 22 g). Significantly more nut length variation was detected among than within *A. mexicanum* trees ($F_{44,1017} = 45.8$, $P < 0.0001$) in the year of the experiment. More vigorous (i.e. larger size, greater number of leaves, etc.) *A. mexicanum* trees tend to produce larger nuts (Brewer and M. Rejmánek unpubl.), and infructescences with larger nuts tended to have more nuts per infructescence ($R^2 = 0.39$, $P < 0.0001$, $n = 45$ infructescences, each from separate trees). Individual trees having extreme nut sizes appear to bear the same size class of nut among infructescences and from year to year (Brewer pers. obs.); a long-term study is underway to quantify this observation.

Length of undamaged *A. mexicanum* nuts is significantly positively correlated with other nut and seed attributes (Table 1). As expected, the experimental size categories based on length differed significantly with respect to fresh mass and length of nuts, seeds and embryos (Table 2). Large nuts have a significantly greater proportion of pericarp than do small nuts ($P = 0.0002$; Table 2). The proportion of each nut that is comprised of pericarp is significantly positively associated with total nut mass ($R^2 = 0.337$, $P < 0.001$, $n = 434$), but the relationship does not appear to be isometric (Proportion pericarp = $0.265 + 0.034 \times \text{Nut weight} - 0.001 \times \text{Nut weight}^2$; $R^2 = 0.337$); the slope of the regression decreases with increasing nut weight.

Nuts that have damaged, and rotting, endosperm and dead embryos constituted 32% of nuts, on average, per tree (SD = 27.9%, $n = 45$ trees). Approximately 50% of those nuts with damaged endosperm had clearly visible holes of less than 1 mm diameter in the sides of the nuts. Insect-damaged nuts with visible insect holes were not significantly different in length from damaged nuts without visible holes ($t_{234} = 0.53$, $P = 0.59$). Lengths of intact (Kolmogorov-Smirnov $\chi^2 = 4.87$, $df = 2$, $P = 0.18$) and damaged ($\chi^2 = 1.34$, $df = 2$, $P > 0.99$) nuts were normally distributed as separate groups.

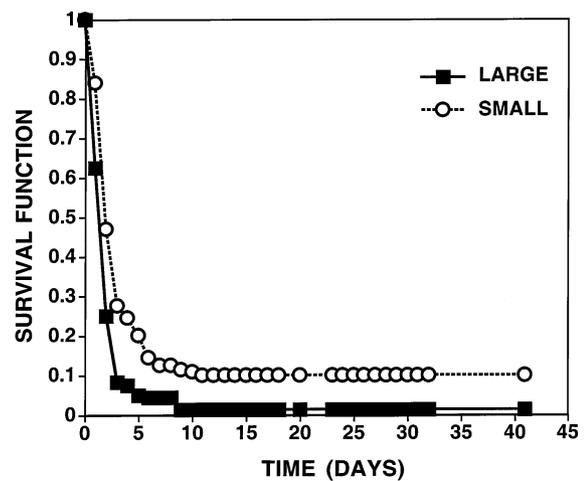


Fig. 2. Survival of large and small *Astrocaryum mexicanum* nuts in 20 enclosures over 41 days. Survival functions differed significantly using log-rank ($\chi^2 = 77.1$, $df = 1$, $P < 0.0001$) and Breslow-Gehan-Wilcoxon ($\chi^2 = 77.6$, $df = 1$, $P < 0.0001$) tests. Final survival at the end of 41 d was significantly greater for small nuts than large nuts ($\chi^2 = 10.50$, $df = 1$, $P = 0.0006$).

Nuts damaged by insects (mean = 43.3 mm length, SE = 0.33, $n = 337$ nuts), regardless of whether or not exit holes were visible, were significantly smaller than intact nuts (mean = 48.0 mm, SE = 0.22, $n = 725$; paired $t_{35} = 8.23$, $P < 0.0001$). The proportion of nuts (per infructescence) damaged by insects, however, showed no significant relationship with total mean nut size per infructescence ($R^2 = 0.056$, $P = 0.11$, $n = 45$ trees) or mean intact nut size ($R^2 = 0.00037$, $P = 0.90$, $n = 45$ trees) – a proxy for potential nut size for a given tree. Insects appear to attack nuts before they have completed development. Observations on immature infructescences often reveal insect-damaged seeds that are empty or that have rotting, undeveloped endosperm (Brewer pers. obs.). None of the damaged mature nuts had any visible frass or insect larvae present, indicating that these insects leave the nut before the insects (and nuts) complete their development, although beetle larvae can sometimes be found inside nuts that have been on the ground for long periods of time (Brewer pers. obs.). Infructescences with fewer nuts tended to have significantly lower overall mean nut length ($R^2 = 0.39$, $P < 0.0001$, $n = 45$ trees). No significant relationship between the proportion of nuts attacked by insects (per infructescence) and total number of nuts per infructescence was found ($R^2 = 0.004$, $P = 0.68$, $n = 45$ trees).

Nut removal rates

Overall, 99.7% of the large and 90% of the small seeds had been removed at the end of the experiment. Removal rates were significantly greater for large than small nuts (Figs 2, 3), using both the log-rank ($\chi^2 =$

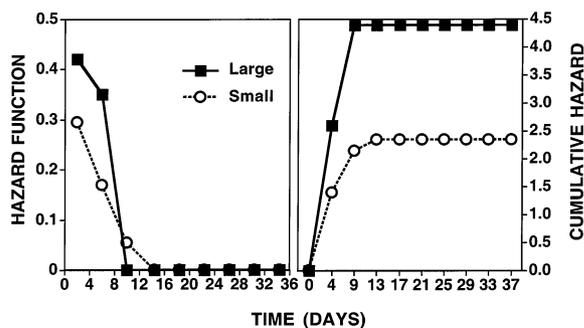


Fig. 3. Hazard and cumulative hazard functions for large and small nuts of *Astrocarylum mexicanum*. The hazard function is the interval-specific mortality of a nut at a given time interval, given that it has survived to the start of that interval. Cumulative hazard shows the rate at which the hazard function changes over time.

77.1, $df = 1$, $P < 0.0001$) and Breslow-Gehan-Wilcoxon ($\chi^2 = 77.6$, $df = 1$, $P < 0.0001$) tests. Although the proportion of nuts that were killed after removal was similar between large and small nuts (see below), small nut survival was significantly greater than large nuts ($\chi^2 = 10.5$, $df = 1$, $P = 0.0006$).

Small-scale heterogeneity in removal rates was also evident. Some exclosures had nearly all of their small nuts remaining after all of their large nuts were removed within several days. Other exclosures experienced removal of both large and small nuts each day, yet proportionately fewer small nuts were taken each time period. Furthermore, even when nut size was taken into account, exclosures differed significantly from each other in their survival functions (log-rank test; $\chi^2 = 187.8$, $df = 19$, $P < 0.0001$; plots not shown), indicating that removal rates and overall removal of *A. mexicanum* nuts varied significantly in space.

Nut fates

No significant effect of nut size on fate was detected (Table 3). On average per exclosure, small rodents buried 11%–16% of the nuts removed from the exclosures (Fig. 4). No significant difference in percent found (by the author) of large and small nuts, 71.3%

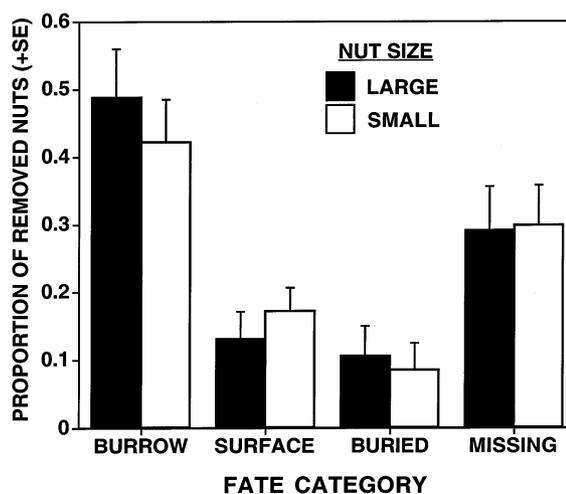


Fig. 4. Mean proportion (+SE) of *Astrocarylum mexicanum* nuts that were removed from exclosures, in four fate categories: burrows of the small rodent *Heteromys desmarestianus*, in cover ("surface", e.g. palm leaf sheaths, duff piles, etc.) on the surface of the forest floor, buried < 2 cm deep by *Heteromys desmarestianus*, and missing. The proportions of large and small nuts are not significantly different within fate categories (MANOVA, for the effect of size $P = 0.81$).

and 76.3%, respectively, was detected (Wilcoxon signed-rank $Z = 1.29$, $P = 0.20$). Reanalysis of the data under the assumption that all missing nuts had been taken into burrows did not change the outcome of the comparison of fates of nuts by size (statistics not shown).

After one year, all of the large nuts that had been buried were removed and not reburied, and were presumably killed ($n = 16$ nuts). Four small nuts, from three non-adjacent exclosures, remained where they had been buried ($n = 13$ small nuts buried). One of these nuts was rotten. The three other nuts had germinated seeds: one of these had died before developing a shoot, the other two appeared healthy and had a root system and unexpanded leaves. The difference in survival from predation of the buried large and small nuts was significant ($\chi^2 = 5.71$, $df = 1$, $P = 0.017$), although with a very conservative continuity correction the difference was marginally insignificant ($\chi^2 = 3.49$, $df = 1$, $P = 0.062$).

Table 3. Multivariate analysis of variance of the proportion of *Astrocarylum mexicanum* nuts of large and small size classes removed from exclosures ($n = 20$), according to their actual fates. ANOVAs for the proportion of seeds having each fate are presented. Fates = buried, taken to surface cover, to burrows, or missing.

	df	Buried		Surface		Burrows		Missing	
		MS	F	MS	F	MS	F	MS	F
Size ^a	19	0.013	0.36	0.065	1.06	0.071	0.57	0.23	1.87
Exclosure ^b	1	0.14	3.96*	0.095	1.55	0.21	1.63	2.69×10^{-7}	2.24×10^{-6}
Residual	19	0.36		0.061		0.13		0.12	

All F values are not significant ($P > 0.05$) unless noted with an asterisk.
* $P = 0.002$; ^a $P = 0.81$, Wilks' $\lambda = 0.91$; ^b $P < 0.001$, Wilks' $\lambda = 0.0060$.

Table 4. Repeated measures analysis of variance for the effect of size on the mean distances that *Astrocaryum mexicanum* nuts were moved from exclosures (replicates), using fates (buried, taken to surface cover, or to burrows) as the repeated measure.

Source of variation	df	MS	F	P
Size	1	19.9	1.1	0.32
Fate	2	74.4	2.8	0.08
Exclosure	19	17.7	2.6	0.63
Size × Fate	2	6.1	1.2	0.79
Size × Exclosure	16	6.7	0.3	0.99
Fate × Exclosure	23	26.8	1.0	0.52

Distances of nuts removed from exclosures

The overall effect of size on distance that nuts were taken was not significant using repeated measures ANOVA ($P = 0.32$; Table 4, Fig. 5). However, taking into account the exclosures from which the nuts were removed, small nuts tended to be taken farther than large nuts when they were buried, although the sample sizes of buried seeds were small ($n = 16$ and 13 large and small seeds, respectively) ($P = 0.046$, $df = 2$, paired $t = 4.50$). Small nuts were taken farther on average when moved into cover on the surface of the forest floor, but the difference was not significant ($P = 0.41$, $df = 6$, paired $t = 0.88$). For seeds taken to burrows, no significant difference between the seed-size classes was detected on the first day of removal (for the respective exclosure) ($P = 0.48$, $df = 11$, paired $t = 0.72$) or for

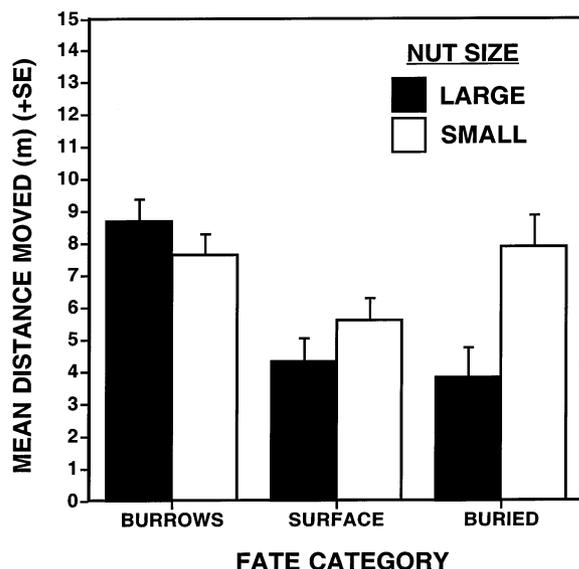


Fig. 5. Mean distances (+SE) that *Astrocaryum mexicanum* nuts were moved by small rodents. Sample sizes for each size and fate are given inside their respective bars. The overall effect of size was not significant (repeated measures ANOVA, $P = 0.77$). For buried seeds the effect of size on distance moved was marginally significant ($P = 0.046$, paired $t = 4.50$, $df = 2$). All other fates were not significant (ns; all $P > 0.4$).

removal over the time of the experiment ($P = 0.82$, $df = 14$, paired $t = 0.24$). The effect of fate on the distance that nuts were taken was not significant when mean distances per exclosure, for each nut size, were used in the repeated measures analysis ($P = 0.08$, Table 4, Fig. 5).

Discussion

Seed size preferences

This study supports the predictions that, in general, large seeds experience greater predation pressure (e.g. Janzen 1969, 1971, Harper 1977) from mammals than small seeds. Small seeds of *A. mexicanum* had both greater total survival and lower mortality rates than did large seeds (Figs 2, 3). These results are congruous with some studies indicating that small rodents prefer species with large seeds (in tropical forest: Adler 1995; in temperate communities: Reynolds 1958, Abbott 1962, Reichman 1975, 1979, Podolsky and Price 1990, Reader 1993, Hoffman et al. 1994), although this preference is far from being a universal trend (in tropical forest: Osunkoya 1994, Blate et al. 1998; in temperate communities: Price 1983, Price and Podolsky 1989, Kerley and Erasmus 1991, Meiners and Stiles 1997, Kollman et al. 1998).

Although this study focused on the effects of small rodents on seed survival, the opportunity to study predispersal seed predation by insects was taken during the analysis of nut-size variation. Such predation reached nearly one third of the number of nuts produced. The insect responsible for such damage emerges or dies before the nut can drop to the ground, apparently before endosperm development is complete (Brewer pers. obs.). The proportion of *A. mexicanum* nuts (per tree) damaged by insects in this study was not correlated with the mean size of nuts per tree. This lack of correlation suggests that insects do not select *A. mexicanum* nuts by size, are not capable of assessing nut size early in the development of the infructescence, or are less able to penetrate developing nuts that are destined to become large. It is also possible that these insects simply select nuts based on position in the infructescence, which is known to determine the size of seeds in some species (e.g. Waller 1982, Stanton 1984a). However, insect-damaged seeds were significantly smaller than undamaged seeds. The presence of insects thus appears to hinder nut development rather than indicate selection of smaller nuts within an infructescence. For the rodents, the most important outcome of insect predation of the nuts is that insect-infested nuts end up being significantly smaller than insect-free nuts and are usually devoid of edible endosperm.

Conditions affecting seed size preferences

Why did a significant proportion of small *A. mexicanum* nuts remain undisturbed in exclosures (Fig. 2), even when they were the only choice available? All else being equal, large seeds offer more energetic return for foraging effort and should be preferred by mammals when food availability is relatively high, as it is during the wet season when most *A. mexicanum* trees are in fruit. When food availability is very low, size may become unimportant in selection of seeds by rodent foragers under dietary stress. The cause of a preference for large *A. mexicanum* seeds by *H. desmarestianus* may simply be an innate preference, may reflect some environmental condition not measured during the experiment, or perhaps may be related to predation of seeds by insects.

The latter possibility raises an important issue for future research. Spiny pocket mice do not avoid insect-damaged *A. mexicanum* nuts altogether (Brewer pers. obs.). Experienced individual foragers, however, may have learned to avoid small nuts, because of the higher probability that these nuts contain no or lower energetic reward with respect to endosperm and/or insect larvae. By the time an *A. mexicanum* nut that has been attacked by insects falls to the forest floor, a substantial portion of its endosperm as well as its insect are missing. The reverse may be true where vertebrates preferentially feed on insect-containing fruits over insect-free fruits (Redford et al. 1984). Learning behavior in food selectivity has been well documented in other animals (e.g. Kamil et al. 1987).

Selection of different-sized nuts was clear in some exclosures that experienced complete (or near complete) removal of large and not small nuts, and in other grids where large nuts were removed before small nuts. Strong variation among grids in ratios of large to small seeds removed, as well as the proportion of seeds that were buried, points to behavioral differences among individuals of *H. desmarestianus* in the selection and handling of seeds (Table 3); *H. desmarestianus* is the exclusive handler of *A. mexicanum* nuts at the study site. Strong variation among individual rodents with respect to proportions of seeds hoarded has been documented in temperate systems as well (Clarke and Kramer 1994, Jenkins et al. 1995). The causes of these differences in foraging behavior among individual rodents may have important ecological and evolutionary consequences (Hayes and Jenkins 1997, Jenkins 1997), possibly including the spatial structure of tree recruitment, and therefore should be explored in future studies.

H. desmarestianus can also be considered a central place forager, in addition to being a scatterhoarder, since it often uses burrows as a base from which to forage and as a larder for hoarding food. According to central place foraging theory, foragers should select

larger food items with increasing distance from the central place (Orians and Pearson 1979, Schoener 1979). In this study, distance to burrow was not significantly different between the two sizes of *A. mexicanum* seeds that were taken to burrows, either at the beginning or the end of the experiment. Thus, in this study, central-place-foraging theory does not necessarily explain the individual variation observed in seed-size preferences.

Implications for tree recruitment

For seedling recruitment, the consequences of this preference for large seeds will depend on the other fates that befall large and small seeds. Most *A. mexicanum* nuts were larder hoarded deep (> 40 cm, pers. obs.) in burrows (Fig. 4), where they will likely be eaten or will die as seedlings that are unable to reach the soil surface (100% of viable seeds planted 40 cm deep in the field or greenhouse died as seeds or as unemerged seedlings, Brewer unpubl.). *A. mexicanum* nuts may also be moved on the soil surface to cover. None of these seeds escaped predation, although that does not preclude the possibility that a small fraction of all of the forest seeds taken to this fate may escape predation. Nuts taken to burrows and places with cover may therefore be assumed to represent predation, but no significant difference was found in the proportions of each size of seeds that experienced these two fates, even though large nuts were preferred.

For large Neotropical rodents (e.g. agoutis), scatter hoarding rates appear to increase with interspecific seed size (Forget et al. 1998). In this study, however, there was no difference in the proportions of *A. mexicanum* nuts of each size that were scatter hoarded – the only known fate that may enhance seed survival. Thus, there was no compensation (in later survival) to larger seeds for being removed at a higher rate and overall amount than small seeds. Scatter hoarding benefits small more than large *A. mexicanum* nuts in two ways. First, when scatter hoarded, small nuts are moved farther than large nuts (Fig. 5). Longer distances moved may mean that small nuts will also be buried at lower densities than large nuts. Distance- or density-dependent seed predators are therefore less likely to discover these nuts (Janzen 1970, Connell 1971, Stapanian and Smith 1978). In contrast, larger seeds and/or more preferred food items tend to be scatter hoarded farther from the source in temperate systems (Hurley and Robertson 1987, Vander Wall 1995, Leaver and Daly 1998). Second, large and small nuts were equally likely to be buried, and therefore potentially protected from predators. Burial of seeds decreases the probability that seeds are eaten (e.g. Stapanian and Smith 1978, Estrada and Coates-Estrada 1986, Forget 1990, 1991, 1992, Vander Wall 1990, Hulme 1993, 1994), but does not affect the

probability of *A. mexicanum* seed germination during the wet season (Brewer unpubl.). Although the sample size of buried nuts was small, nearly one third of the small *A. mexicanum* nuts that were buried by *H. desmarestianus* remained buried long enough to germinate, but all of the buried large nuts were recovered by small rodents. It is not clear whether such burial equally protects large and small seeds from naïve foragers as opposed to the foragers responsible for scatter hoarding the seeds. In temperate systems, rodents are more likely to discover and dig up large seeds than small seeds (see reviews by Reichman 1981, Hulme 1993). Whether or not this pattern holds true for tropical forests will require additional studies focusing on the effects of burial on seed survival. Despite the potential proportional benefit of survival to small nuts that fall beneath the tree, the fewer small nuts are actually removed from beneath the parent tree – and potentially buried – than are large nuts.

What effects the rodents' preference for large nuts has on tree recruitment – from seeds in the tails of the seed-size distribution in *A. mexicanum* – also depends in part on the relative survival of the resulting seedlings. Large nuts of *A. mexicanum* have greater endosperm and embryo masses (Table 2), and therefore confer a possible advantage to their seedlings. Large seeds of other species give their seedlings an initial advantage in establishment, and seed size is positively correlated with other plant characters that may be of ecological importance during seedling establishment (see reviews by Foster 1986, Westoby et al. 1992, 1996). Moreover, larger seeds may produce individuals that have greater vigor and possibly fitness (e.g. Austenson and Walton 1970, Stanton 1984b, 1985), although data for tropical trees are scarce (but see Howe and Richter 1982).

For *A. mexicanum* a potential reproductive tradeoff may accompany producing a small or large seed. Large seed size may be a benefit for seedling vigor but may incur the relatively high costs of predation and smaller dispersal distances. Future research should test whether such tradeoffs exist within species by examining long-term survival of seedlings from experimentally and naturally dispersed seeds of different size, and whether or not differential predation and dispersal can interact with seed size to effect variation in plant recruitment. Examining the mechanisms behind choice of seeds by animals is also an important path of the investigation of seed size and predation/dispersal, because variation within populations of seed predators, due to sex, maturity, and foraging experience, might also interact with seed size variation to generate patterns of plant recruitment. As small rodent populations fluctuate, for example, so might the proportion of individuals experienced enough to distinguish between seeds of low and high food value. Because of the high predation rates of seeds – especially those buried by small rodents – future

experiments that track seed fates will encounter the challenge of having enough replicate seeds to be able to detect any patterns that may be due to seed-size variation.

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