

14 The Role of Seed Size in Dispersal by a Scatter-hoarding Rodent

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Introduction

Many species of birds and mammals hoard food from locally abundant, ephemeral sources to conserve it for future use (Vander Wall, 1990). The hoarding strategies they follow cover a range bounded by two extremes. 'Larder-hoarders' store their food in one or few caches, each containing much food. 'Scatter-hoarders', in contrast, store food by dispersing it in small amounts among many spatially separated caches. Where larder-hoarding requires active defence or some other mechanism to prevent robbery of the food by competitors, scatter-hoarding relies on spreading the risk of robbery (Vander Wall, 1990). This chapter is about the long-term effects of scatter-hoarding seeds in the upper layer of soil, as is practised by a variety of granivorous birds and mammals.

Scatter-hoarding of seeds has potential advantages to plants. First, it involves transport

away from the parent plant, an area that is not only occupied already by the species, but is also often hostile for seeds and seedlings because of pathogens and herbivores associated with adult conspecifics (Janzen, 1970; Hammond and Brown, 1998). This transport is the dispersal needed for the colonization of new sites. Secondly, scatter-hoarding takes seeds away from an area in which they are concentrated and scatters them throughout the surrounding area, isolating individual seeds or small groups of seeds from their siblings. Scattering increases the independence of fates among individual seeds. It reduces the risk of density-dependent mortality, such as consumption by wild pigs and oviposition by granivorous insects (Wilson and Janzen, 1972). It also increases the probability of seeds hitting suitable sites if such sites are patchily distributed in the environment. Thirdly, burial of seeds in the topsoil reduces the probability of other seed-eaters finding and killing the seed

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(Stapanian and Smith, 1984; Vander Wall, 1993) and often preserves seeds in better condition for germination and establishment (see Vander Wall, this volume).

The main reason that the advantages of scatter-hoarding are considered potential is that scatter-hoarding has a price: scatter-hoarding animals often recover most hoarded seeds for consumption. Thus, seeds must escape the hoarder in order to profit from scatter-hoarding. For the parent plant, scatter-hoarding is advantageous if the benefits of some seeds surviving outweigh the costs of all others being eaten, i.e. if scatter-hoarding increases the total number of seeds establishing.

Many plant species seem to depend on scatter-hoarding animals for seed dispersal (Vander Wall, 1990). These species, mostly trees, produce larger, more nutritious seeds and in smaller numbers than most plants with other dispersal modes (Smith and Reichman, 1984; Vander Wall, 1990; Leishman *et al.*, 1995; Hammond *et al.*, 1996). Also, large-seeded plants tend to be more seasonal in fruit production than smaller-seeded species and synchronously mature fruit when scatter-hoarding peaks (e.g. Smythe, 1970; Jackson, 1981). These observations have led to the hypothesis that these plant species are adapted to scatter-hoarding: their reproductive strategy has been shaped by scatter-hoarding animals over evolutionary time (Smythe, 1970; Smith and Reichman, 1984; Hallwachs, 1994).

The adaptive explanation of the scatter-hoarding dispersal syndrome is appealing. Many experiments have shown that seed mass, a central characteristic of plant reproductive strategy, is indeed heritable and sensitive to selection (e.g. Cober *et al.*, 1997; Gjuric and Smith, 1997; Malhotra *et al.*, 1997) and so is seed nutrient composition (e.g. Brandle *et al.*, 1993; Rebetzke *et al.*, 1997). Yet the hypothesis of adaptation is difficult to test. Fossil records can be used to determine whether seed size has increased over evolutionary time (e.g. Eriksson *et al.*, 2000). Vander Wall (2001), for example, concludes from fossil records that tree genera currently dispersed by scatter-hoarding animals in the temperate zone have indeed increased seed size since the Palaeocene (~60 million years ago). Still, whether such increases

occurred in response to scatter-hoarding animals cannot be determined. What we can do, however, is test the underlying assumption that scatter-hoarding animals impose selective pressure on reproductive traits (in particular, seed size) through their behaviour. Such pressure is a prerequisite for selection towards the production of larger seeds.

Selection towards large seeds

There are several ways in which scatter-hoarding animals could select for larger, more nutritious seeds, all of which assume it is more economical for scatter-hoarders to create and manage a smaller supply of large, nutritious (i.e. high-value) seeds rather than a large supply of small, less nutritious seeds.

First, the likelihood of scatter-hoarders encountering a seed may increase with seed value, because animals may discover high-value seeds more easily or because they may focus their foraging on known sources of high-value seeds. Secondly, high-value seeds may have higher removal rates, because rodents prefer them. Such a preference could give high-value seeds a greater probability of being harvested at all (see Waite and Reeve, 1995). Thirdly, the decision of what to do with a seed after it is harvested may depend on seed value. Scatter-hoarding animals usually eat a few seeds during the process of hoarding many others (see Forget *et al.*, this volume). The seeds they store may preferentially be high-value seeds, while low-value seeds are eaten (Hallwachs, 1994). Fourthly, scatter-hoarders may vary how they cache a seed, depending on its value (Stapanian and Smith, 1978, 1984; Clarkson *et al.*, 1986). High-value seeds could thus get stored in more favourable conditions than low-value seeds (i.e. further away, in lower densities, deeper or at better sites). Finally, the storage life of caches could depend on seed value. Scatter-hoarders could use their high-value seed caches at slower rates than low-value caches, saving highest-value seeds for last. Alternatively, high-value seeds could simply be used at lower rates because they have been cached at lower densities and greater depths and are therefore found less easily by both the cache owner and cache thieves (Stapanian and

Smith, 1984; Vander Wall, 1993). In both cases, the result would be higher survival for high-value seeds.

This study

We conducted a field experiment to test possible selective pressures towards higher seed value by scatter-hoarders. We measured how seed value influenced the fate (death or establishment) of seeds offered to the red acouchy (*Myoprocta exilis*, Waylor, 1831), a neotropical rodent that scatter-wards seeds by burying them singly. A second aim was to quantify survival probabilities of seeds harvested and cached by acouchies, because direct proof for scatter-hoarding being beneficial to plants is still remarkably scarce (Jansen and Forget, 2001).

We tested the following hypotheses:

1. Large seeds are more likely to be harvested by acouchies than small seeds.
2. Large seeds are harvested by acouchies more quickly than small seeds.
3. Large seeds harvested by acouchies have a higher probability than small seeds to be cached rather than eaten.
4. Large seeds are cached further away and in lower densities than small seeds.
5. Large seeds are recovered from caches and consumed at lower rates than small seeds.
6. Large seeds have higher survival probabilities than small seeds.

Methods

Site and species

We worked at the Nouragues biological station in the Nouragues Reserve, an undisturbed lowland rain-forest site in French Guiana, 100 km south of Cayenne, at 4° 02' N and 52° 42' W and 100–150 m above sea level. Annual precipitation averages 2900 mm, with peaks in December–January and April–July. The main fruiting season is from February to May (Sabatier, 1985). Bongers *et al.* (2001) give an extensive description of the site.

To isolate the effect of seed value from other seed characteristics that may influence

preferences of animals, such as nutrient composition, secondary compounds, digestibility and odour (Hurly and Robertson, 1986), we took advantage of intraspecific variation in fresh seed mass. Seed wet mass is a good measure of seed value. The nutrient content of seeds is not proportional to seed mass, but larger seeds do contain a larger absolute amount of nutrients and have proportionally less (inedible) seed-coat (Grubb and Burslem, 1998).

We used seeds of *Carapa procera* (*Meliaceae*), henceforth 'Carapa', a canopy tree species reaching up to 25 m height, occurring throughout the neotropics. *Carapa* produces up to 100 large (*c.* 10 cm diameter), five-valved fruits that contain up to 20 large, fatty seeds (Forget, 1996; Jansen and Forget, 2001). Seeds are shed gradually in February–July, but mostly in May, a period of intense seed-hoarding (see Forget *et al.*, this volume). Fruits burst open upon hitting the ground, scattering seeds under the parent tree. Fresh masses of ripe seeds at Nouragues span a more than 20-fold range, from 3 to 65 g (mean = ~21 g).

Carapa seeds are sought after by acouchies, especially in lean years (Forget, 1996; Jansen and Forget, 2001). The red acouchy, *Myoprocta acouchy* (Erxleben, 1777), is the most common scatter-hoarding animal in French Guiana. It is a caviomorph rodent, 33–39 cm length, and weighs 1.0–1.5 kg (Emmons and Feer, 1990). Acouchies store seeds, their main food, by burying them in shallow caches in the topsoil. They are perfect scatter-hoarders, because they harvest seeds one by one and store them in single-seeded caches. This behaviour led Morris (1962) to introduce the term scatter-hoarding. Acouchies, like agoutis (*Dasyprocta*), scatter-hoard seeds and fruits from many plant species and are therefore considered important seed-dispersers. Acouchies are diurnal, with peak activity at dawn and dusk. They have territories of about 1 ha (Dubost, 1988).

Seed removal

Between 19 April and 24 May 1999, during the peak hoarding season, we established 11 feeding plots of 60 cm × 60 cm below or

near reproductive *Carapa* trees. Plots were separated by > 100 m, the average acouchy territory radius according to Dubost (1988), to ensure replication with different individuals. On each plot, we placed 49 *Carapa* seeds that varied widely in fresh mass. Seed masses did not differ between plot samples (Kruskal–Wallis test: $\chi^2_{10} = 14.0$, $P = 0.18$). Our samples had a higher average seed mass than a random sample taken from the same population in 1995 (analysis of variance (ANOVA): $F_{1,420} = 31.4$, $P < 0.001$). While this random sample was skewed to larger seed values (skewness $g_1 = 0.68$ with $SE = 0.08$; kurtosis $g_2 = 1.02$), our sample was approximately normally distributed ($g_1 = -0.17$ with $SE = 1.11$; $g_2 = 0.14$). Seeds were collected a few days before placement from the local population of reproductive *Carapa* (~25 trees). Seeds were weighed, thread-marked (see below), given a number for identification and randomly assigned to positions in a 7×7 grid in each plot. Varying seed value within plots enabled us to control for differences in detectability associated with seed size and to account for differences between animals and sites. An animal visiting a plot would simultaneously encounter the entire range of seed values and make its choice among them.

We used an automatic video system to observe selection and removal of seeds without the influence of our presence. We monitored visitation, seed selection and seed removal at 3 frames s^{-1} , using a surveillance camera (Philips VCM 6250/00T) and a time-lapse video recorder (Panasonic AG-1070 DC), mounted on a tree at ~1.5 m. Plots and video equipment were set up at night. Automatic recording took place in daylight during the following 1.5 days, during which time practically all seeds were removed. From the videotapes we recorded the identity of the animal taking each seed and the seeds' order of removal. Recordings were not always complete, due to power problems. One plot completely lacked recordings, due to a defect.

Seed fate

Acouchies carry seeds over large distances and bury them with practically no trace. To be

able to retrieve seeds, we attached 1 m of fluorescent green fishing-line with 8 cm of fluorescent pink flagging tape at the end. Acouchies buried these marked seeds but not the line or flagging. Flagged lines protruding from the soil made cached seeds visible up to 10 m. Numbers on the thread marks allowed us to identify seeds without disturbing the cache. Marking seeds in this way is not thought to influence caching behaviour (Forget, 1990), but we cannot rule out the possibility that it influenced our estimate of survival. We believe that any such influence would probably decrease survival, thereby generating conservative estimates of survival.

We searched for seeds immediately after plot depletion, 1.5–2 days after establishment of the plots. We attempted to retrieve all seeds, but stopped after 12 h of searching. We mapped all seed locations, using coordinates of labelled trees (Poncy *et al.*, 2001). Sites of cached seeds were marked with small tags at eye-level on nearby saplings or palms. Flags of caches were covered with leaves to avoid their use by other animals to find caches.

We checked caches at 2, 4, 8, 16, 32, 64 days and 4 months after installation of the plot. We resurveyed the entire area at 32 and 64 days to relocate seeds that had disappeared from caches, because such seeds are often recached rather than eaten (Jansen and Forget, 2001; see also Hoshizaki and Hulme, this volume; Vander Wall, this volume). Whether recaching was done by the cache owner or by a competing acouchy or agouti could not be determined, but this is of no importance from the perspective of the seed. Likewise, we could not determine whether caches were depleted by scatter-hoarding rodents or by peccaries (*Tayassu* spp.), unless seeds had been recached.

The seed fates we distinguished were: still cached, eaten, (re)cached, mark lost (i.e. thread mark separated from seed) and not found. We also noted germination and looked for remains of seedlings around depleted caches. Both acouchies and agoutis sever the epicotyl (including the meristem) when digging up germinated seeds (Jansen and Forget, 2001). Seeds treated in this way cannot form a new seedling, but they do form scar tissue and stay alive for many months as

'zombies'. In this way, acouchies transform rapidly germinating *Carapa* seeds into a non-perishable food suitable for long-term storage. Since *Carapa* seeds normally germinate within a few weeks, we considered seeds that disappeared from caches between day 64 and 4 months as dead.

Analyses

Effects of seed mass were tested using regression techniques and ANCOVA, in which we treated distance, masses and survival as continuous (co)variables and seed fate as a categorical variable. Because the area surrounding plots was unlimited, we could not calculate cache densities. Instead, we calculated 'cache isolation': the median distance to caches from the plot of the seed's origin. This measure behaves as the inverse of cache density and is less sensitive to neighbouring caches being overlooked (for instance, because seeds lost their thread mark) than nearest-neighbour distance.

Distances were \log_{10} -transformed to attain normality, except in quantile regressions (see below). Survival time was \log_2 -transformed to obtain time steps of uniform size. Seed fresh mass was \log_{10} -transformed, unless stated otherwise, because we assumed that the importance for rodents of a given increase in mass would be greater in light seeds than in heavy seeds.

Fates of seeds within plots were not independent, especially in the harvesting phase, when one animal handled all seeds in a short time span; what happened to one seed had consequences for what happened to others in the same plot. We used plots, not seeds, as experimental units for all situations in which strong dependence occurred. We used regression techniques to deduce one value per plot describing the trend within each plot: the regression coefficient β (or B) weighted by the inverse square of its standard error (SE),

$$\text{weighted } \beta_i = \beta_i \times \text{SE}_i^{-2} \times \frac{1}{n} \sum_{i=1}^n \text{SE}_i^{-2}$$

where i is the plot number and n is the number of plots. These values were tested against

$\beta = 0$ using the t -statistic at $\alpha = 0.05$. Overall trends were calculated as the mean of all plot values (G. Gort, Wageningen, 2000, personal communication).

Analyses of post-dispersal survival were done using logistic and Cox proportional-hazard regression models, mostly on pooled data, because sample sizes within plots were too small for plot-level analysis. There may have been some dependence of post-dispersal seed fate within replicates, but we feel that this should not be too problematic for post-dispersal trends, because the foraging decisions concerned are separated in time and were probably made by more than one animal.

We used quantile regression (Koenker and Bassett, 1978) to investigate heteroscedastic variation in errors. Quantile regression gives a more complete picture of the data distribution than common (least-squares) regression and is more robust against the influence of outliers. It can help recognize limiting factors and estimate their effect (Scharf *et al.*, 1998; Cade *et al.*, 1999). We calculated regression quantiles using the least absolute deviation (LAD) quantile regression procedure in BLOSSOM (Midcontinent Ecological Science Center, 1998). The significance of quantile regression factors was tested using rank-score tests, in which the statistic T_{observed} was tested against a distribution of T obtained from 5000 permutations (Slauson *et al.*, 1994). All other analyses were performed with the SPSS 10.0.5 statistical package (SPSS, 1999).

Results

Seed removal

All seeds were removed within 1.5 days, except for three seeds, which were removed 1–2 days later (Table 14.1). Video recordings showed that 50 seeds were taken by white-lipped peccaries (*Tayassu pecari*, 25 seeds), collared peccaries (*Tayassu tajacu*, 13 seeds) and red-rumped agouti (12 seeds). These seeds were excluded from further analyses. We treated all of the remaining 489 seeds as removed by acouchies, including 113 without video proof.

Because all seeds were removed, hypothesis 1 was not confirmed: large seeds did

Table 14.1. Fates of *Carapa procera* seeds harvested by red acouchies (*Myoprocta exilis*) in French Guiana.

	Plot											Total
	1	2	3	4	5	6	7	8	9	10	11	
Initial seed fate												
Cached	40	23*	37	23	17	4	39	44	20	23	34	304
Eaten	1	7	8	1	11	5	4	1	7	6	7	58
Mark lost	1	1	2	1	12	11	1	2	0	0	0	31
Not found	7	18	2	24	9	4	5	2	10	4	8	93
Total (<i>n</i>)	49	49	49	49	49	24 [†]	49	49	37 [†]	33 ^{†‡}	49	486
Initial fate of seeds recovered from primary caches												
Recached	3	3	8	7	4		6	6	3		5	45
Eaten	4	3	11	7	6	2	18	25	5	17	26	124
Not found	32	16*	16	8	3	2	8	7	7	5	3	107
Mark lost	1		2	1	4		6	6	5			25
Not recovered		1 [§]					1			1		3
Total (<i>n</i>)	40	23	37	23	17	4	39	44	20	23	34	304
Cache half-life (days)	5	3	6	5	21	23	6	18	4	22	23	9
Ultimate seed fate												
'Survived'		1 [§]	1	1	3		1			1		8
Eaten	5	13	23	16	21	7	27	27	14	27	42	222
Incomplete record	36	18*	21	16	8	2	17	19	16	5	5	163
No record	8	17	4	16	17	15	4	3	7	3	2	96
Total (<i>n</i>)	49	49	49	49	49	24 [†]	49	49	37 [†]	36 [†]	49	489

*Includes one seed of unknown weight.

[†]Not including 50 seeds that were taken by peccaries or agoutis.

[‡]Not including three seeds that were removed later than the first census.

[§]The seed had established a seedling at 4 months.

not have a greater probability of being taken by acouchies. The exact sequence of removal (hypothesis 2) was also independent of seed size (*t*-test on weighted linear regression coefficients for ten plots: $t_9 = 0.55$, $P = 0.593$; does not include one plot lacking video data). The exact sequence of removal was strongly related to the position of seeds within the plot: edge, second row or centre (ANOVA: $n = 376$, $F_{2, 373} = 37.0$, $P < 0.001$). Even when we pooled data and controlled for position, there was no effect of seed size on sequence of removal (ANCOVA: $n = 375$, $F_{1, 372} = 0.15$, $P = 0.70$). The animals spent little time selecting seeds (8 s on average), usually taking the first seed they encountered.

Hoarding versus consumption

We located 362 seeds the day after dispersal. The vast majority (84%) was cached; relatively few seeds (16%) were eaten (Table 14.1). The probability of being cached versus being eaten increased with seed mass at the population level, which confirms hypothesis 3 (Fig. 14.1; logistic regression: $n = 303$ cached, 58 eaten, Wald = 17.0, $P < 0.001$). The probability of being cached also depended on the order of removal: the later seeds were taken from a plot, the lower the probability of being cached ($n = 226$ cached, 46 eaten, Wald = 3.9, $P = 0.049$). Both effects, however, were not significant at the plot level, due to small numbers of eaten seeds.

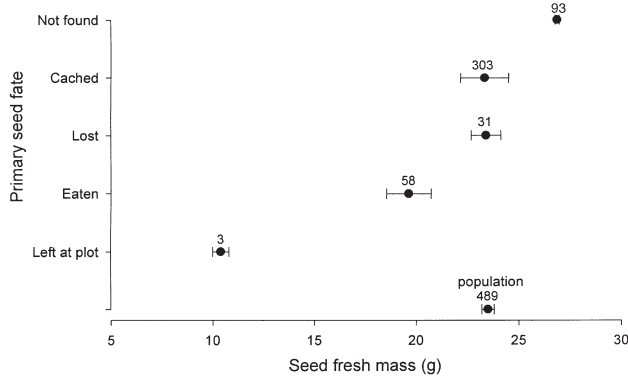


Fig. 14.1. Effect of seed fresh mass on treatment of 488 *Carapa procera* seeds by red acouchies (*Myoprocta exilis*). Data from 11 plots are pooled. Mean values (\pm SE) of seed fresh mass for different fates at 1 day after dispersal, and sample sizes. Seeds found eaten had lower masses (*t*-test: $n = 58$, $t_{57} = -3.5$, $P = 0.001$), while seeds that were not found at all were heavier (*t*-test: $n = 93$, $t_{92} = 4.7$, $P < 0.001$) than the population mean.

Cache spacing

The distance at which we found acouchy caches immediately after dispersal was highly variable, both within and among plots. The nearest cache was found < 1 m from the plot, the furthest was 124 m away. Cache distance increased with seed size, as predicted by hypothesis 4 (*t*-test on weighted linear regression coefficients for ten plots: $t_9 = 7.7$, $P < 0.001$; does not include a plot that was largely depleted by peccaries and hence had few caches). Most variation in cache distance, however, was not explained by seed mass (Fig. 14.2).

There was also great variation in spatial isolation of acouchy caches, both within and among plots. Larger seeds were more widely spaced than smaller seeds, in support of hypothesis 4. Both cache isolation (*t*-test on weighted linear regression coefficients for ten plots: $t_9 = 5.5$, $P < 0.001$; does not include plot depleted by peccaries) and nearest-neighbour distance ($t_9 = 5.0$, $P < 0.001$) increased with seed mass. However, there was no positive effect of seed mass on cache isolation when we took into account cache distance ($t_9 = -1.9$, $P < 0.096$), not even in the pooled data (multiple regression: $\beta_{\text{distance}} = 0.81$, $F_{1,300} = 883$, $P < 0.001$; $\beta_{\text{mass}} = -0.25$, $F_{1,300} = 10.9$, $P = 0.001$; model $F_{2,300} = 271$, $P < 0.001$, $R^2 = 0.75$). Apparently, wider spacing was a direct result of further dispersal of

larger seeds without an additive effect of seed mass.

Cache exploitation

The lifetime of caches was highly variable. While many caches were depleted within a week, some were still intact 4 months after dispersal. Cache lifetime increased with isolation (Fig. 14.3; Cox regression: $n = 295$ depleted, nine censored, Wald = 9.7, $P = 0.002$). Cache lifetime also increased with cache distance from the source (Wald = 6.0, $P = 0.015$), but the distance to source did not explain variation additional to cache isolation. Seed mass did not affect cache lifetime (Wald = 1.0, $P = 0.32$), contradicting hypothesis 5.

Recovery of seeds, however, did not necessarily lead to seed consumption. Many seeds were recached or were not found again (Table 14.1). Larger seeds had a higher probability of being recached rather than eaten (logistic regression: $n = 124$ eaten, 45 recached, Wald = 4.4, $P = 0.035$). Consumed seeds were found much closer to the cache site than recached seeds (means = 12 m and 31 m, respectively; ANOVA: $F_{1,167} = 25$, $P < 0.001$). This and the fact that the probability of losing seeds increased with distance, due to our inability to search thoroughly at greater distances, suggest that most of the seeds not found were actually recached at greater distances. If

we assume that lost seeds were indeed recached, the probability of escaping immediate consumption increased with seed mass

more strongly (logistic regression: $n = 124$ eaten, 151 recached or lost, Wald = 11.3, $P = 0.001$). This result supports hypothesis 5.

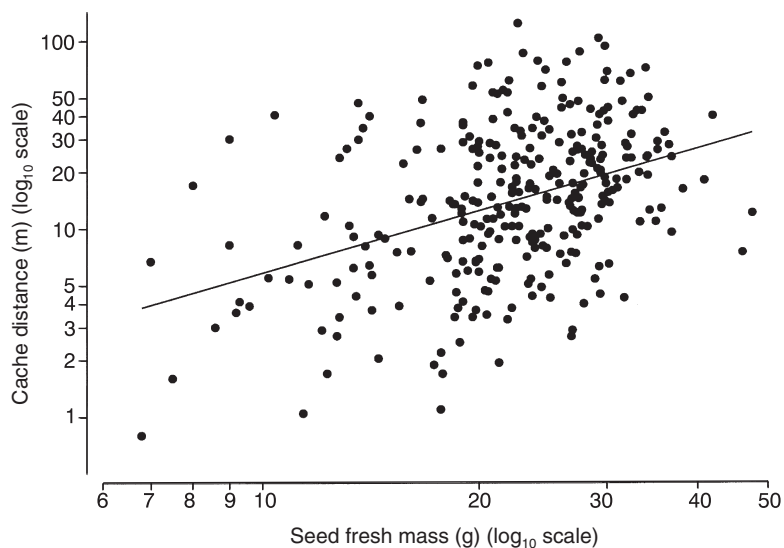


Fig. 14.2. Effect of seed fresh mass on the distance from the source of acouchy caches found 1 day after dispersal (\log_{10} scales). Pooled data ($n = 303$) for 11 plots. Cache distance increased with seed fresh mass (ANCOVA: mass $F_{1, 291} = 79$, $P < 0.001$; plot $F_{10, 291} = 16$, $P < 0.001$; model $F_{11, 291} = 22$, $R^2 = 0.45$). The increase is significant at the plot level (see text).

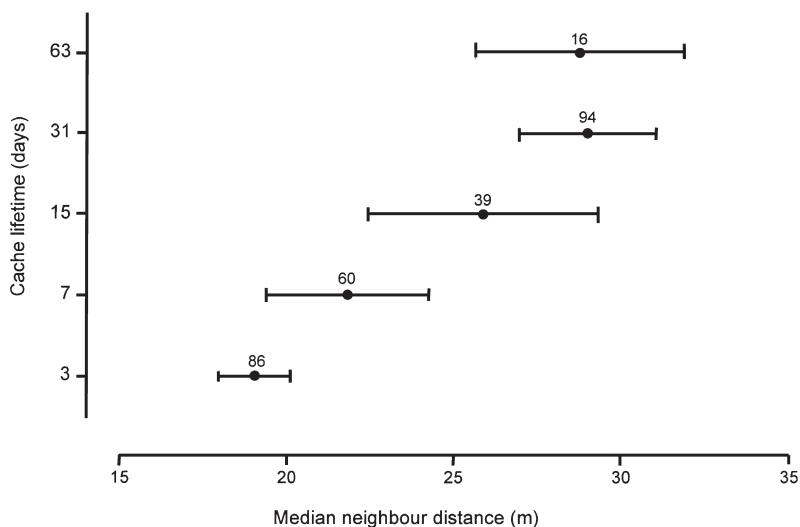


Fig. 14.3. Effect of cache isolation (median distance to other caches) on cache lifetime, i.e. the time until a cache was found depleted (approximately on \log_2 scale). Pooled data ($n = 304$) from 11 plots. Mean values (\pm SE) of isolation for different cache lifetimes, and sample sizes. Cache isolation positively affected the survival probability of caches (see text).

Ultimate seed fate

During subsequent searches and monitoring, we found additional seeds, mostly in caches at great distances. In total, we obtained complete or partial records of seed fate for 393 seeds (80%). The remaining seeds lost their thread mark (35 seeds or 8%) or were never found (61 seeds or 12%). We were able to determine the ultimate fate of 235 seeds (Table 14.1). Of these, only one (0.5%) established a seedling. The remaining seeds were eaten (95%), had been displaced after germination and probably became ‘zombies’ (1%) or were still cached without an epicotyl (4%). Probably, the latter seeds had germinated and become ‘zombies’ without our noticing. Fates of all seeds are summarized in a seed-fate pathway diagram (Fig. 14.4), following Price and Jenkins (1986).

Acouchies and other granivorous mammals gradually ate cached seeds. Seeds eaten

tended to be lighter than those kept in stock (i.e. cached plus recached), but the difference was significant only during the first 2 weeks after dispersal (Fig. 14.5). The more rapid consumption of small seeds caused a gradual increase of the stock’s mean seed mass. The total proportion of seeds with unknown fate also increased over time, because some seeds were lost every time they were handled. Lost seeds tended to be heavier than the stock mean mass. If those seeds were (re-)cached at great distances (see above), the increase of the stock mean mass was even greater than our estimate.

Overall, seed mass strongly affected the fate pathways of seeds and how long seeds were kept in stock (Fig. 14.6; *t*-test on weighted Cox regression coefficients from 11 plots: $t_{10} = -4.1$, $P = 0.002$). The ultimate probability of survival increased with seed mass, as posited by hypothesis 6 (logistic regression: $n = 8$ survived, 480 eaten or lost, Wald = 4.1, $P = 0.043$).

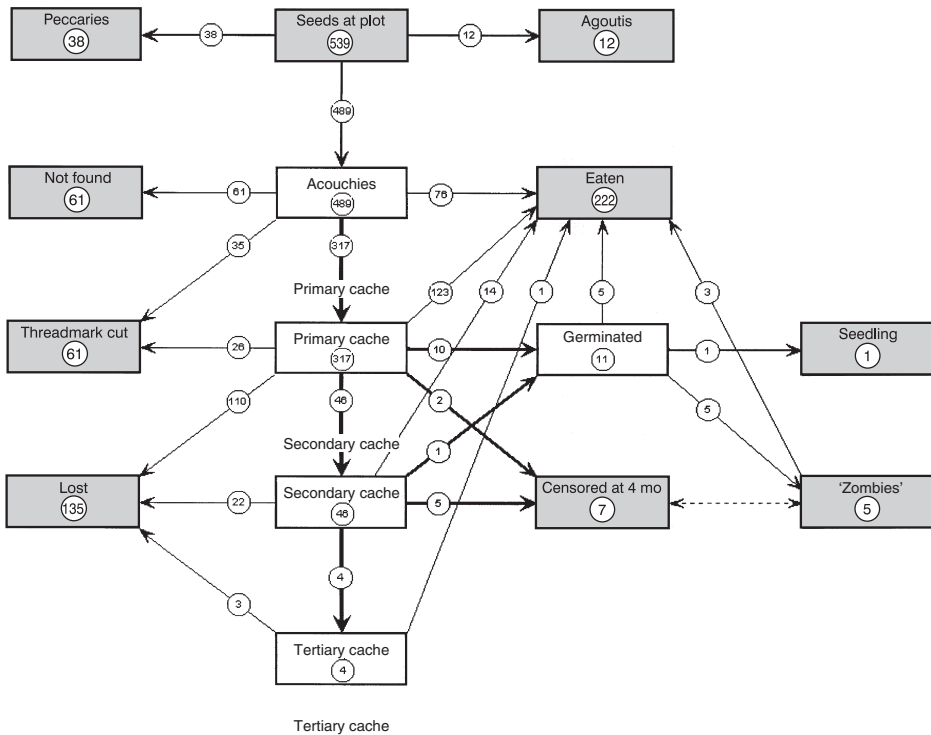


Fig. 14.4. Fate pathways of 539 *Carapa procera* seeds placed in 11 plots in territories of different red acouchies.

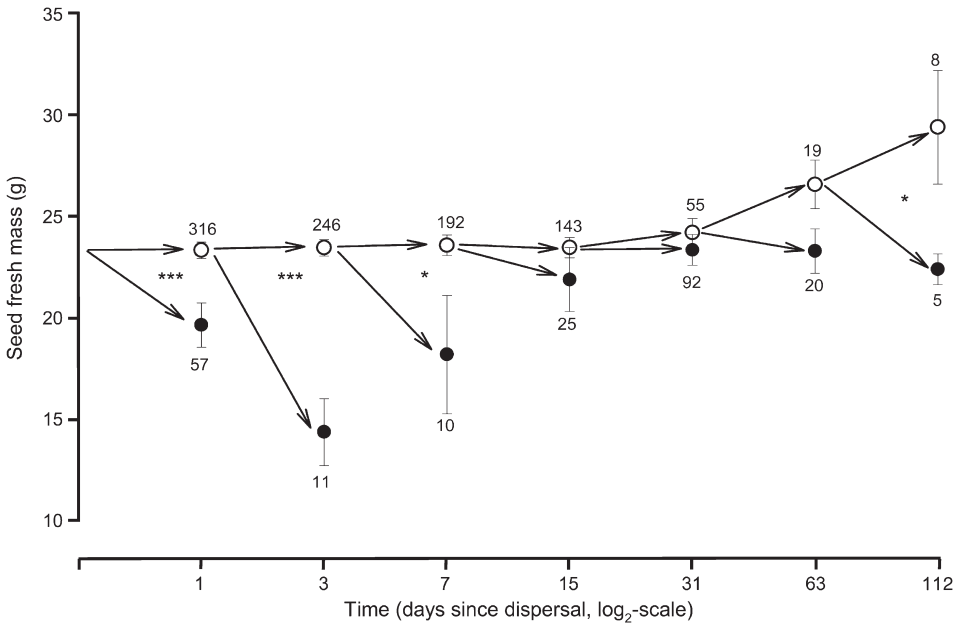


Fig. 14.5. Change of mean mass of cached seeds over time (approximately on \log_2 scale). Pooled data from 11 plots. Filled circles are seeds that were found eaten at time t but still cached at time $t - 1$, hollow circles are seeds that were still cached. Seeds that were taken from caches but not found are not shown. Numbers are sample sizes. Significance levels are of t -tests of differences in mean mass within pairs: ***, $P < 0.001$; *, $P < 0.05$; Seed mass increased the probability of seeds remaining cached rather than being eaten.

Discussion

The belief that many large-seeded tree species depend on scatter-hoarding for regeneration has been largely based on the observation that scatter-hoarding animals were the only vectors for movement of seeds away from the parent tree, where all seeds were killed by seed predators (Jansen and Forget, 2001). There are few studies that measure fate pathways of individual seeds (Chambers and MacMahon, 1994; but see Vander Wall, 1994, 1995a,c; see also Vander Wall, this volume; Hoshizaki and Hulme, this volume). Our study is the first to determine ultimate seed fates of scatter-hoarded seeds in a tropical rain forest, with a known dispersal vector and over distances far beyond 50 m.

We found direct evidence that scatter-hoarding granivores such as acouchies can effectively disperse large-seeded trees. Almost 500 *Carapa* seeds removed by acouchies resulted in one established seedling. This may

seem unsubstantial, but 0.2% success is not trivial, given the large numbers of seed produced during a tree's reproductive lifespan (Janzen, 1971; Hallwachs, 1994). Furthermore, caviomorph rodents have high rates of mortality (Dubost, 1988; Hallwachs, 1994) and the death of an acouchy could greatly increase the survivorship of its cached seeds. This prediction could be verified by experimental removal of acouchies from their territories after scatter-hoarding. A more general idea of dispersal effectiveness requires estimations for more years, including years both with high and with low food availability.

Selection towards larger seeds

Our results indicate that scatter-hoarding can result in selection towards larger seeds: the chance of small seeds surviving 4 months was negligible compared with that of large seeds.

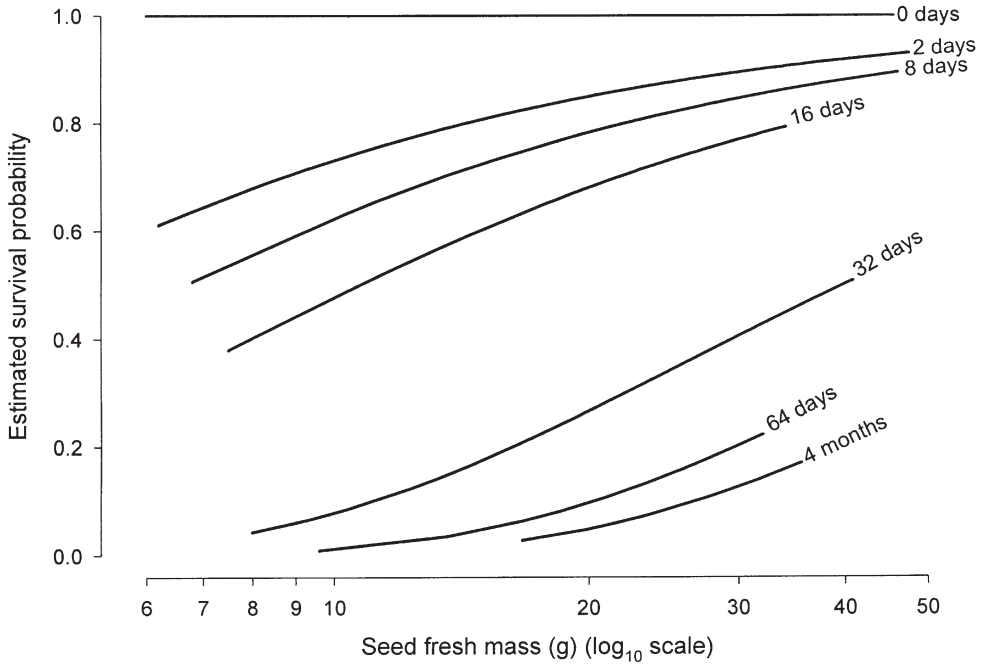


Fig. 14.6. Effect of seed mass (\log_{10} scale) on seed lifetime. Survival probability curves as a function of seed mass according to the Cox regression model (see text for further explanation).

Larger seeds were more likely to be cached by acouchies rather than eaten (Fig. 14.1) and were cached further away (Fig. 14.2). Isolation of caches increased with cache distance and translated into longer lifetimes of caches (Fig. 14.3). If removed from their cache, larger seeds were also more likely to be recached than eaten. Overall, larger seeds were consumed at a lower rate than small seeds (Fig. 14.5), which resulted in a higher net probability of survival and seedling establishment for large seeds (Fig. 14.6). Seed mass, however, did not affect the speed and probability of harvest by acouchies.

As was hypothesized by Smith and Reichman (1984), preference for large seeds by scatter-hoarding animals could result in the evolution of larger-seeded crops by providing better dispersal for large-seeded individuals than for small-seeded individuals of the same species. Because we varied seed size within crops, our experiments provide no evidence for acouchies discriminating among seed crops of different seed size. Experiments by Hallwachs (1994) with agoutis in Costa Rica,

however, did. Hallwachs found that the proportion and absolute numbers of acorns cached (rather than eaten) by agoutis was higher at large-seeded trees than at small-seeded trees, although the latter had greater numbers of seeds. She also found that artificial seeds (pieces of coconut) from large-seeded crops were cached further away than artificial seeds from small-seeded crops. Acouchies are likely to behave similarly, because they are closely related to agoutis and remarkably alike in behaviour (Smythe, 1978; Dubost, 1988). Another example comes from Waite and Reeve (1995), who found that scatter-hoarding grey jays discriminated among sources of different quality; the birds cached substantially more raisins from a large-item source than from a small-item source when source types were made available on different days.

Selectivity in removal

There are many examples of selectivity by scatter-hoarding animals based on food value

(e.g. Smith and Follmer, 1972; Bossema, 1979; Reichman, 1988; Jacobs, 1992; Lucas *et al.*, 1993). The best support for the idea that acouchies should be selective comes from Hallwachs (1994), who found that agoutis in Costa Rica preferred heavier seeds if a range of seed masses was available. Why didn't the acouchies in our study discriminate against small seeds during removal?

One possible explanation comes from models of optimal foraging, in which animals maximize the net rate (Stephens and Krebs, 1986) or efficiency (Waite and Ydenberg, 1994a,b) of hoarding, with time as the primary limiting factor. The risk of food competitors claiming the food source, for example, increases with the time spent on source depletion. According to these models, non-selectivity should occur if the difference in rate of energy gain between large and small seeds is too small for selectivity to pay off. In our study, the amount of time spent per unit food value could have been almost constant because acouchies' investment in caching increased with seed value. However, we think that time was not the primary limiting factor. Acouchies used approximately 1 day to deplete a plot, usually interrupting their work for several hours. The number of seeds removed by competitors was nevertheless quite modest. Competition appeared unimportant at the time-scale of plot depletion.

A more plausible explanation of non-selectivity is that food availability is the limiting factor. Having sufficient food stored is crucial for survival during the period of food scarcity. Selectivity would limit the amount of stored food. Acouchies can afford the luxury of being selective only once a sufficiently large food supply is cached. Perhaps the animals in our study had to cache every *Carapa* seed they found to achieve an adequate supply. We predict that acouchies will show selectivity when food is abundant. Because speed of removal determines the probability of escaping seed predation by peccaries and insects and the probability of being cached rather than eaten, such selectivity would intensify selection towards larger seeds.

Hoarding versus consumption

Scatter-hoarding rodents often eat some seeds while storing many others (e.g. Hallwachs, 1994; Peres and Baider, 1997). We found that larger seeds were more likely to be stored by acouchies than small seeds and were more likely to be recached after recovery from their original cache. Hallwachs (1994) also observed that the proportion of acorns and of pieces of coconut cached by Costa Rican agoutis increased with their size. All small acorns were eaten. Apparently, large seeds are more suitable for storage than smaller ones.

Large seeds may be more frequently cached than small seeds because they have a longer storage life. Large seeds, for example, could be more persistent to drought, which causes *Carapa* seeds to decay (Ferraz-Kossmann and De Tarso Barbosa Sampaio, 1996), due to lower relative permeability to water (lower ratio of surface to volume). Likewise, lower relative water absorption could delay germination of larger seeds. Large seeds might also be more easily managed, as larger reserves take longer to be depleted by a seedling, giving animals more time to intervene and turn seeds into 'zombies', which can be conserved for several months. An alternative explanation is that a preference for larger seeds reduces the number of caches that acouchies must remember and manage for a given mass of food. This explanation, however, immediately begs the question of why acouchies never put more than one seed in a cache.

Cache distance

Our finding that larger seeds were cached at greater distances than small seeds and further away from other seeds agrees with models of optimal cache spacing (Stapanian and Smith, 1978; Clarkson *et al.*, 1986). These models predict that scatter-hoarders hide higher-value food in lower densities (i.e. further away) to compensate for the greater risk of such food being stolen by competitors. Several field studies have confirmed that larger seeds are

cached at greater distances (Stapanian and Smith, 1984; Hurly and Robertson, 1986; Hallwachs, 1994; Jokinen and Suhonen, 1995; Vander Wall, 1995b; Forget *et al.*, 1998). Most of these studies, however, were based on interspecific variation in seed size. Food value was thus confounded with other differences among species, including nutrient composition, secondary compounds, digestibility, taste and odour (Hurly and Robertson, 1986). Our study controlled for extraneous variables by varying seed value within species, as did two earlier studies: Hurly and Robertson (1986) observed that whole groundnuts were cached by red squirrels further away than half groundnuts, and Hallwachs (1994) found that the proportion of seeds cached beyond her sight by agoutis increased with seed size.

Constraints on cache distance?

The relationship between cache distance and seed mass was much weaker than expected

from cache optimization models. A large proportion of variation in cache distance remained unexplained (Fig. 14.2). What might explain this variation? The untransformed data showed that the range of cache distances varied with seed mass: the maximum distance increased with seed mass, while the minimum remained almost constant. Moreover, the maximum distance seemed to have an optimum at ~29 g, beyond which it dropped off again. The resulting polygonal shape of the scatter diagram could indicate limiting factors (Scharf *et al.*, 1998; Cade *et al.*, 1999).

We investigated this so-called 'envelope effect' (Goldberg and Scheiner, 1993) using quantile regression on pooled data for eight quantiles (Scharf *et al.*, 1998). First, we tested whether regression quantiles had an optimum by calculating the contribution of the cubic and the quadratic factor to the model. Both were significant for none of the quantiles, implying that the apparent 'optimum' could simply be an artefact of low numbers of extremely large seeds (stepwise regression with

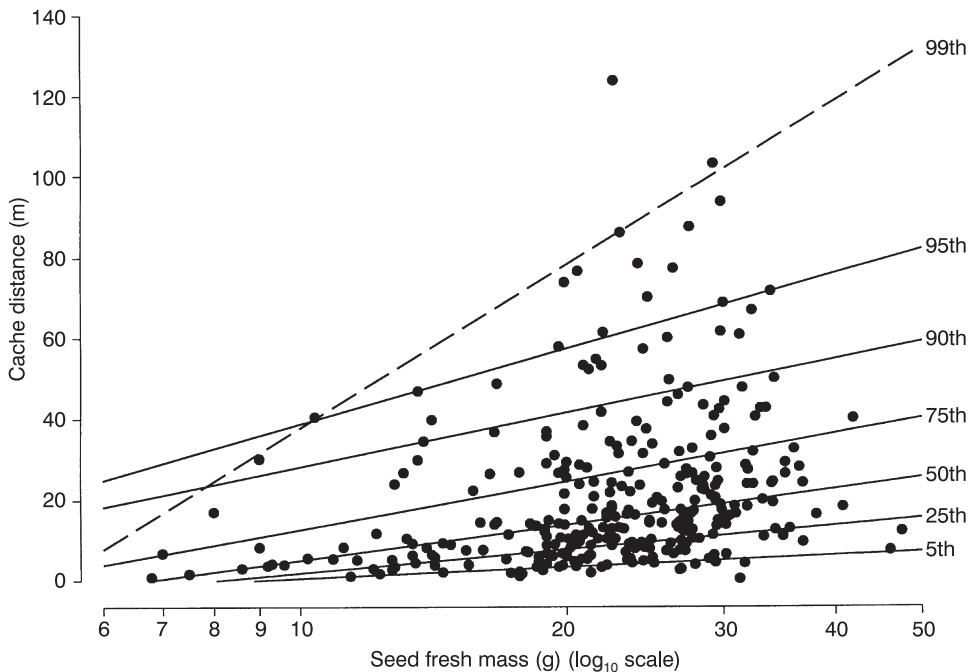


Fig. 14.7. Effect of seed fresh mass (\log_{10} scale) on the distance from the source of acouchy caches found 1 day after dispersal. Pooled data ($n = 303$) for 11 plots. Plotted lines are significant quantile regressions for seven values of τ (see Table 14.2).

Table 14.2. Quantile regressions of cache distance on fresh mass of *Carapa procera* seeds scatter-hoarded by red acouchies (*Myoprocta exilis*). Data from 11 replicate plots were pooled ($n = 303$). Estimates of β_0 and β_1 are given for models $y = \beta_0 + \beta_1 \cdot x$ (A) and $y = \beta_0 + \beta_1 \cdot \log_{10} x$ (B) with y for cache distance (m) and x for seed fresh mass (g). P values for $H_0: \beta_1 = 0$ were obtained from 5000 permutations and rank-score tests (Slauson *et al.*, 1994). Model B quantile regressions gave a better fit and are shown in Fig. 14.7. A third model, $y = \beta_0 + \beta_1 \cdot x + \beta_2 \cdot x^2$, did not produce a better fit for any of the quantiles.

Model	Quantile	β_0	β_1	T_{observed}	$P(\beta_1)$
A	5th	-0.5	0.17	0.045	< 0.001
	10th	-1.5	0.29	0.049	< 0.001
	25th	-1.9	0.45	0.071	< 0.001
	50th	-3.4	0.81	0.076	< 0.001
	75th	10.8	0.70	0.021	< 0.01
	90th	21.9	0.91	0.025	0.052
	95th	26.6	1.33	0.055	< 0.05
	99th	12.9	3.10	0.095	0.091
B	5th	-9.1	9.6	0.043	< 0.001
	10th	-12.1	12.6	0.045	< 0.001
	25th	-17.7	19.6	0.067	< 0.001
	50th	-24.4	29.4	0.072	< 0.001
	75th	-26.8	39.5	0.024	< 0.005
	90th	-16.3	44.5	0.028	< 0.05
	95th	-23.5	62.2	0.062	< 0.05
	99th	-97.3	135.0	0.114	0.06

backward elimination of factors). We then calculated quantile regressions of cache distance on seed mass and on \log_{10} -transformed seed mass (Table 14.2). Regression coefficients (β_1) were significant at $\alpha \leq 0.10$ for all quantiles in both models, and increased with τ , implying that most of the variation in distance occurs in the upper quantiles. Quantile regressions with seed mass \log_{10} -transformed gave the best fit (Table 14.2, Fig. 14.7). Potential cache distance was clearly far greater for large seeds than for small seeds.

These results suggest that cache distance is limited by some constraint related to seed value, described by the upper regression quantiles. This constraint could correspond to the investment at which the net benefit of seed caching is zero, as suggested by Hurly and Robertson (1987). Cache spacing being governed by a constraint is in disagreement with the models of Stapanian and Smith (1978), Clarkson *et al.* (1986) and Tamura *et al.* (1999), in which cache distance is distributed around an optimum investment, depending on seed size, at which the net energy gain is maximized. A similar 'envelope effect' appears in Hallwachs's

(1994) data of agouti cache distance versus acorn size.

Although our data do not prove that potential cache distance had an optimum at 25–30 g of fresh mass rather than continuously increasing with seed mass, the idea of an optimum seed mass makes sense. There must be a seed mass beyond which handling and transport become increasingly difficult and expensive for acouchies. Selection by acouchies will not be directional towards ever-larger seeds but, instead, should stabilize at an optimum. Studies including very large seeds in test samples are needed to test this possibility.

Cache isolation

That large seeds were indeed more likely to be cached far away from other seeds agrees with optimal cache-spacing models (Stapanian and Smith, 1978; Clarkson *et al.*, 1986). However, we found no additive effect of seed mass on dispersal distance. Thus, large seeds were not spaced out more widely than small seeds with the same dispersal distance. We conclude that

the two-dimensional cache-spacing pattern is a result of variation in one-dimensional dispersal distance and dispersal direction. Cache isolation and cache density, in other words, are by-products of dispersal, rather than characteristics directly manipulated by acouchies.

Escape from a classic trade-off

The fact that acouchies carried larger seeds further than small seeds is logical from the point of view of foraging theory. However, the result of larger seeds having better dispersal than small seeds is in disagreement with the classic theory of a size–number trade-off between dispersability and vigour (Smith and Fretwell, 1974). This theory assumes that the allocation of nutrients to reproduction is limited and that plants must find an optimal balance between producing large seeds and producing many seeds. Reasoning that small seeds have a higher probability of being effectively dispersed, a need for effective dispersal would select against producing large seeds. Our findings suggest that dispersability in species dispersed by scatter-hoarding animals selects towards the production of large seeds. Scatter-hoarding enables these plant species to produce larger seeds than species with other dispersal modes.

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