CHAPTER 26

SCATTERHOARDING RODENTS AND TREE REGENERATION

Patrick A. Jansen and Pierre-Michel Forget

1. Introduction

Tree seeds that drop down to the rainforest floor, either naked or embedded in fruit pulp, often disappear after a while. Many authors refer to this phenomenon as seed predation, implicitly assuming that the seed is destroyed by seedeaters such as rodents or ungulates (Forget *et al.* 1998). However, not all seed removal is by seedeaters. Many species of animals remove seeds while feeding on what is around seeds rather than on the seeds themselves. Terrestrial birds, mammals and reptiles ingest seeds while feeding on fallen fruit (e.g. Fragoso 1997, Érard & Sabatier 1988), tortoises ingest seeds while feeding on dung of frugivorous mammals (B. Josseaume unpublished data.), and dung beetles take and bury seeds with dung (Shephard & Chapman 1998, Andresen 1999, Feer 1999). All these animals may bring viable seeds into favourable conditions.

Removal even by seedeaters need not be detrimental to seeds. Some species of mammals and birds store important amounts of seed for later use in periods of food scarcity by creating numerous spatially scattered caches with few seeds each, behaviour called 'scatterhoarding' (Morris 1962). Several animals hoard seeds by hiding them in shallow caches in the soil. If such seeds, for whatever reason, happen to escape consumption by the hoarder, they may be in a good position to germinate and establish. Thus, even seedeaters may function as seed dispersers that enhance seed survival.

This chapter considers the role of scatterhoarding animals in tree regeneration in the Guianan rain forest. In this region, two important scatterhoarding animals are the Red acouchy, *Myoprocta exilis* (Wagler 1831), and the Red-rumped agouti, *Dasyprocta leporina* (L. 1758) (Dubost 1988), both caviomorph rodents. It has been hypothesised that these rodents and their food plants are mutually dependent; the rodents would not survive periods of food shortage without the food provided by the trees, while the tree species would not survive without the rodents dispersing their seed (Smythe 1978). Whether the rodents are indeed obligate mutualists for certain species of trees is highly relevant for sustained management of forest ecosystems, since interdependence could necessitate protection of animal populations (Jansen & Zuidema 2001).

Assuming that rodents bring seeds to safer sites, the fact remains that they do so in order to eat the seeds later. This paradox of seed predators functioning as seed dispersers has been the basis of much research in French Guiana. Our aim is to review evidence of scatterhoarding rodents being favourable to seeds, and to identify lacunas in the existing

knowledge. First, we will discuss the question of how important scatterhoarding rodents actually are in terms of quantities of seeds removed and scatterhoarded, and what dispersal patterns they create. Secondly, we consider scatterhoarding from the viewpoint of the rodents on the one hand and the trees on the other. To evaluate whether the interaction between rodents and trees is mutualistic, we will try estimating the net contribution of scatterhoarding to regeneration by subtracting the costs of scatterhoarding. Finally, we briefly discuss some evolutionary aspects of the interaction between trees and rodents and point out directions for further research.

2. Patterns of seed removal and dispersal

Sabatier (1983) and Forget (1990) showed that the large seeds of *Vouacapoua americana* (Caesalpiniaceae), a canopy tree species that had often been assigned to the 'unassisted dispersal' group, were removed by rodents once they had been shed. Later, similar results were found in other tree and liana species that produce fruits with large edible seeds but no edible fruit pulp, such as *Carapa procera* (Meliaceae) (Forget 1996), *Astrocaryum paramaca* (Palmae) (Forget 1991) and *L. alba* (Chrysobalanaceae). Rodents also appeared to remove a great variety of other seed species. These included large seeds of bird- and monkey-dispersed species, such as the Myristicaceae (Forget & Milleron 1991) and Sapotaceae (Forget *et al*. Chapter 25), as well as large seeds of bat-dispersed species, such as the Lecythidaceae and Fabaceae (Forget 1992, 1993).

Seed removal by acouchies and agoutis is also important in terms of numbers. Jansen and co-workers laid out more than 100 batches of 10-50 large seeds and video-recorded animal activity during the following day(s). In nearly all cases, scatterhoarding rodents were the first seedeaters seen at the plots. Acouchies accounted for almost 90 per cent of cases of discovery, agoutis for less than 10 per cent. Other important seedeaters, especially in terms of seed quantities removed at a time, were collared peccaries (*Tayassu tajacu*) and white-lipped peccaris (*T. pecari*). These wild pigs eat seeds on the spot, crushing and killing all seeds but the minute (Feer *et al.* Chapter 21). Other seedeaters, such as spiny rats (*Proechimys cuvieri* and *P. guianensis*) and Guianan squirrels (*Sciurus aestuans*) rarely removed seeds. The former both scatterhoard (Forget 1991, Hoch & Adler 1997, Adler & Kestell 1998) and larderhoard seed (Guillotin 1982), while the latter scatterhoard seed in trees.

Removal experiments and video recordings have shown that acouchies and agoutis eat few of the seeds in situ. Forget (1996) found that the percentage of *C. procera* seeds in experimental batches consumed in situ was approximately 10-20 per cent, and decreased during the season. Removal rates of seed species also differ between years, depending on the absolute and relative seed availability and the relative food value of seeds (Smallwood & Peters 1986). In lean years, all consumable seed species are removed quickly, with strong competition for seeds between acouchies, agoutis and peccaries. In years of high production, the animals concentrate on preferred species (see e.g. Fig. 1). In 1996, for instance, removal of *C. procera* seeds did not set off until production of the preferred species *Licania alba* had ceased completely. Then, the animals became interested in taking even old and germinated seeds of *C. procera*.

Forget (1990) laid out thread-marked *V. americana* seeds, and searched for them after their disappearance. He discovered that a great proportion (70 %) was scatterhoarded in the direct surroundings, threadmarks protruding from the soil enabling relocation of the buried

seeds. Further experiments with threadmarks and video cameras showed that the great majority of all seed species taken by acouchies or agoutis are scatterhoarded. Both species typically cache seeds individually, scattered throughout the forest surrounding a seed tree, at distances ranging from 0.5 up to 125 m (*C. procera* seed cached by an acouchy in 1999). Seeds are buried at depths from zero to 6 cm below the soil surface and are always covered with leaves. Caches are often near or in objects such as palm cones, tree logs and trunks (Smythe 1978, Forget 1990, Vander Wall 1990), and tangles of branches and lianas.
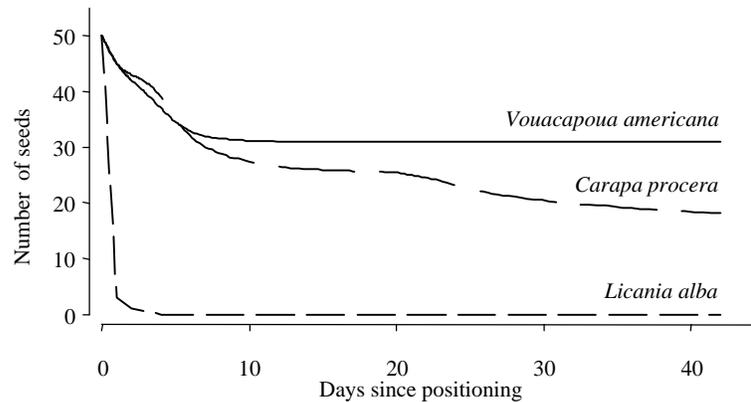

Figure 1. Removal of three seed species by scatterhoarding rodents. 50 seeds per species were placed at the forest floor along a transect with 2m inter-spacing, and 6m between conspecific seeds (*n* = 50). Nouragues, May 1996, (P.A. Jansen and A. Siepel, unpublished data)

Figure 2 shows a typical layout of caches of *Licania alba* seed after one week of video-recorded seed removal by an acouchy from an artificial feeding plot. The missing seeds may have been stored beyond the 50 m search radius.

3. The animal perspective

Hoarded seeds seem to play a vital role in the life cycle of acouchies and agoutis. Most hoarding is done during the wet season, when the majority of tree species fruit; i.e. February to April and especially May to June in French Guiana (Forget 1996). The exploitation of hoarded seeds especially occurs during the period of seed scarcity that follows. The animal's dependence on hoarded supplies during this period seems very strong. The seed proportion in the agouti diet increases when fewer seeds are available. In the leanest period of the year, seed matter even makes up almost 75% of the agouti stomach content (Henry 1999). The rodents literally live on their reserves.

Having sufficient hoarded seed available for use at the desired moment is an obligatory yet complicated task, since the rodents are not unique in their interest for the seeds. There is a constant threat of losing stored (and to-be-stored) seed reserves to food competitors, seed perishing and seed germination. Given the vital importance of reliable supplies, agoutis and

acouchies face an enormous pressure to reduce these losses. Therefore, it is imperative that they adopt a profitable strategy of seed caching and cache management.
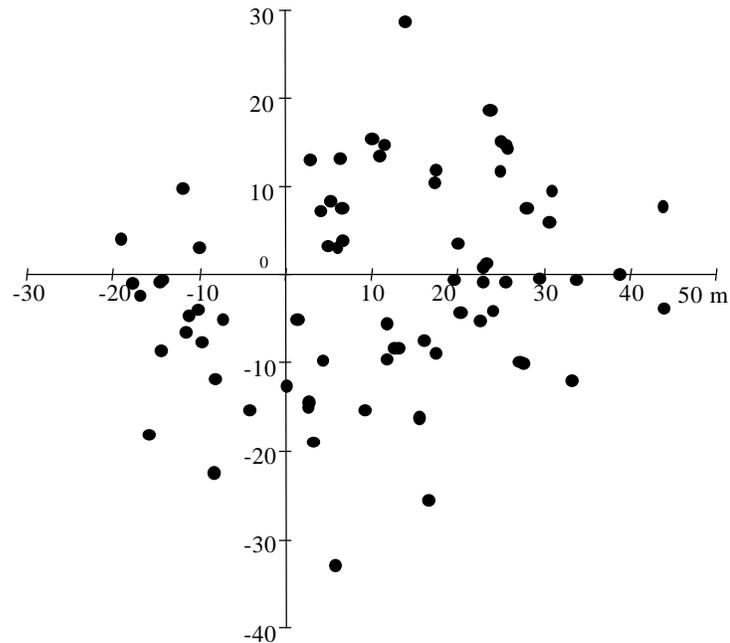

Figure 2. Spacing pattern of *Licania alba* seeds scatterhoarded by an acouchy. 52% of 139 threadmarked seeds taken from an artificial food source (origin) were relocated. Nouragues, May 1996 (P.A. Jansen and A. Siepel, unpublished data).

3.1 SELECTIVITY AND SEED VALUE

The amount of seed scatterhoarders can store is limited not only by seed availability, but also by the hoarder's time and energy budget, the availability of suitable storage sites, and the needs of competing seedeaters. In the face of these limitations, it may pay for animals to be selective in their choice of seed use. Caching efficiency might be increased by caching the most valuable seeds first. Seed value roughly depends on energy/nutrient content and storage life. For short-term hoarding, animals can simply focus on the net energy content (accounting for handling costs). Nuthatches, for example, prefer caching husked sunflower seeds to unhusked ones, since the former yield more net energy as no investment in dehusking is required (Moreno & Carrascal 1995). Long-term hoarding demands a focus on seed value at the desired moment of consumption rather than at time of hoarding. Nutritional content of cached seeds may decrease due to germination (i.e. use of seed reserves by the plant), by insect infestation, or by degradation of nutrients (Post 1992). Therefore, it may be attractive to cache slowly germinating seeds with hard, protective endocarps, or with a high content of secondary compounds that lengthen storage life (Hadj

et al. 1996, Dearing 1997). Tannins, for instance, inhibit insect attack and, thus, help jays conserve acorn supplies (Fleck & Woolfenden 1997).

Both acouchies and agoutis are highly selective in seed caching, for which they have only their territory available. This is reflected by an enormous variation in removal speed of laid-out seed and cache spacing by acouchies for different edible seed species that are found in Guianan forests. Although these seed species differ in an infinite number of aspects, we believe that the rodents select on long seed storage life and high energetic content after storage, which conforms well to the importance of long-term supplies in their life cycles. The preference of *L. alba* and *C. procera* seeds over *V. americana* seeds of comparable fresh weight (Fig. 1), for instance, can be explained by differences in storage life and fat content (Table 1). Furthermore, acouchies clearly select uninfested seeds for caching, as do Gray squirrels (*Sciurus carolinensis*; Steele *et al.* 1996) and Blue jays (*Cyanocitta cristata*; Dixon *et al.* 1997).

TABLE 1. Properties determining nutritional value and storage life of 3 seed species scatterhoarded by acouchies and agoutis. Seeds were collected below parent trees in Nouragues in April 1996. (A. Siepel and P.A. Jansen, unpublished data).

Seed properties	Species		
	Licania alba	*Carapa procera*	*Vouacapoua americana*
Nutritional value	n = 25	n = 63	n = 50
fresh weight (g)	28.3 ± 7.5	22.9 ± 9.1	36.7 ± 10.5
dry weight (g)	9.6 ± 2.6	7.5 ± 3.0	16.3 ± 4.8
fat (g)[1]	2.4	3.7	0.2
Protein (mg)[1]	576	450	652
oligo-saccharids (mg)[1]	384	375	978
Energy (kJ)[1]	206	224	274
Storage life			
Parasitism (%)	9	6	34
seed coat type	hard	Medium	soft
time till germination	>10 mo	2-5 wks	1-2 wks

[1] Chemical analysis was done in duplicate on a mixture of uninfected seeds.

3.2 CACHE SPACING AND CACHE ROBBERY

Rather than actively defending supplies against competitors (which may be effective against other rodents, but not against peccaries and insects), scatterhoarders protect food against thieves through risk spreading or dilution. They anticipate the limited foraging perseverance of their food competitors by making the density of cached seeds so low that the average time needed for competitors to find a second cache after having found one is too long to make further searching worthwhile. The threshold is at the so-called 'giving-up density' (Bowers *et al.* 1993).

Caching a certain amount of seed in lower densities requires a greater area and, thus, a greater investment of time and energy for both transportation and cache recovery compared to caching in higher densities. Stapanian and Smith (1984) and Clarkson *et al.* (1986) reasoned that there is an optimum cache density at which the yield of remaining caches per unit investment is maximal. This optimum density should be different for seeds of different food value, high-value seeds being cached at lower densities than low-value seeds, since a

greater yield merits greater investment in caching as well as in searching by food competitors (Stapanian & Smith 1984).

Larger seed species, which generally have higher food values, indeed tend to be hidden further away and in lower densities than smaller seed species (Stapanian & Smith 1984, Waite & Reeve 1993, Jokinen & Suhonen 1995, Vander Wall 1995b, Forget *et al.* 1998, Leaver & Martin 1998). Acouchies were also found to discriminate between high and low food values. When we supplied an acouchy with *C. procera* seeds covering a wide range of fresh weights, the animal hid heavier seeds further away from the source than lighter ones (Fig. 3).
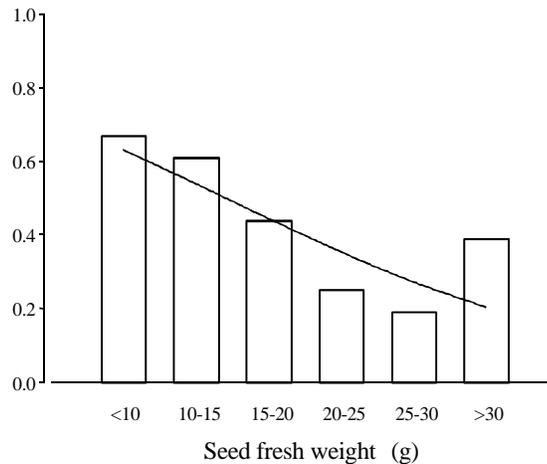

Figure 3. Proportion of *Carapa procera* seed cached within 30 m from an artificial seed source by at least one acouchy. Larger seed were taken beyond 30 m more often than smaller ones (Logistic regression on binary data: Wald=13.7, *p*<0.0001). Nouragues, May 1995, P.A. Jansen, P.M. Forget and L. van der Voort.

Following the same line of optimality reasoning, we may also predict that the optimal cache density will be lower under circumstances of fiercer competition with food competitors, since competition determines how intensively food is sought-after. Food scarcity makes a given seed more valuable and will, thus, lower the optimal cache density. Variation in local fruit availability between years (or areas) can thus lead to great differences in cache densities between years (or areas). Other factors that influence cache spacing include the characteristics of the habitat. Giving-up densities of potential cache thieves may, for instance, be lower in habitats that they can explore more easily. If rodents anticipate such factors, we may expect them to cache seeds at higher densities in habitats that are poorly accessible to pigs, such as treefall gaps with tangles of lianas and tree crowns.

3.3 CACHE PROPERTIES

Seeds are often cached near or in objects, such as logs, and seeds with hard endocarp are more common in soil near such objects than in the open (Kilty 1981). These facts have lead

to the idea that the rodents use objects as visual landmarks to facilitate relocation of cached seeds. This implies the involvement of spatial memory. Although there is plenty of evidence for use of spatial memory by birds (Krebs *et al.* 1996), there is relatively little for rodents. Visual landmarks are used to remember the locations of caches by some species of chipmunks (Vander Wall 1991, Vander Wall & Peterson 1996), squirrels (Jacobs & Liman 1991, MacDonald 1997), kangaroo rats (Jacobs 1992, Barkley & Jacobs 1998), and golden hamsters (Georgakopoulis & Etienne 1994), however not by deer mice (*Peromyscus maniculatus*) (Vander Wall 1993c). Whether acouchies and agoutis use visual landmarks for the recovery of their caches remains to be studied.

An alternative explanation for preferential hiding of seeds near objects is the favourable characteristics of substrates near objects. Some substrates may be easier to dig into, or have better conservation properties. Seeds may, for instance, be less susceptible to spoilage in dryer substrates such as moulded wood along tree logs and accumulations of litter below palms (Vander Wall 1991). Dry substrates may also delay germination and, consequently, the depletion of seed reserves. Moreover, food competitors can have greater difficulty in finding seeds in dry substrates because these blur olfactory cues (Vander Wall 1991, 1993c, 1995c, Jacobs 1992). The extra investment needed for selecting these substrates would be merited by lower cache losses.

The same line of reasoning was followed by Vander Wall (1993a), who predicted that the depth at which seeds are buried increases with seed value. His idea was that food competitors are more tenacious in looking for more valuable seeds, necessitating better caching, while greater seed value at the same time permits hoarders to invest more in hiding. We think that acouchies behave according to this model, as they bury valuable seeds (e.g. *L. alba*) deeper (at up to 6 cm) than less valuable ones (e.g. *V. americana*, mostly hidden right below the surface).

3.4 CACHE MANAGEMENT

Most cached seeds disappear within a few weeks after caching. Forget (1990) found that 57 per cent of 103 cached *V. americana* seeds at three sites disappeared during one month. Likewise, we found that all of 77 *C. procera* seeds cached by (assumingly) one acouchy were gone after one month. The proportion of initial caches left untouched, however, is not a good predictor of the number of seeds surviving. We found that many of the disappeared *C. procera* seeds had been re-cached. We think that most seeds are dug up by the same animals that hid them. However, experiments with man-made caches of thread-marked seed have shown that animals also re-cache seeds stolen from supplies of other individuals (P.A. Jansen and co-workers, unpublished data). We also observed that seeds were re-cached more than once. This has also been observed in the Sierre Nevada where *Tamias amoenus* chipmunks were found to re-cache pine seeds up to four times (Vander Wall & Joyner 1998).

The continuous moving around of seeds seems part of an active management of supplies. Re-arranging caches so shortly after their creation fits to the 'rapid sequestering' strategy (Jenkins & Peters 1992). On discovery of a seed source, an animal will first hide seeds provisionally, as quickly as possible. Only in second instance, after the seed source has been depleted, the animal will optimise cache spacing. This behaviour can be understood if we consider that the risk of losing seed to food competitors will always be greater for exposed seeds than for stored seeds. Agoutis and acouchies may, thus, seek a

compromise between reducing the high short-term risk of competitors taking exposed seeds and reducing the lower longer-term risk of food competitors pilfering seed caches. Kangaroo rats (Jenkins & Peters 1992) and jays (Waite & Reeve 1995) appear to behave in this way.

Another possible reason for rodents to open their caches every now and again is to inspect seed condition. This enables the rodent to judge whether a seed is still good enough to be conserved. Seeds with short remaining storage lives, such as germinated or infested seeds, are better eaten. Re-caching may also refresh the animal's memory of stored seeds.

4. The plant perspective

Scatterhoarding involves seed transportation, scattering, burial and change of the seed micro- and macro-environment. This has several potential advantages to plants. This section discusses how scatterhoarding would increase the chances of seeds surviving, germinating and establishing if the rodents recovered none of the caches they make.

4.1 ESCAPE FROM PREDATORS, PESTS AND SIBLING COMPETITION

The ultimate goal of scatterhoarding - i.e. reducing seed predation and spoilage - combines well with the interest of the parent plant. There are various ways in which the scatterhoarding may reduce seed mortality. First, transportation and scattering moves seeds beyond the direct vicinity of both the parent plant and siblings. This decreases the risk of competition between siblings. Furthermore, it decreases the risk of mortality due to pathogens and pests associated with the parent plant (Janzen 1970, Connell 1971, Hammond & Brown 1998). Most of all, however, it reduces the risk of (distance- and) density-dependent mortality due to all kinds of predators and pests (Janzen 1970, Connell 1971, Hammond & Brown 1998).

In temperate areas, experimentally scatterhoarded seeds indeed disappear more slowly at lower densities (Stapanian & Smith 1984, Clarkson *et al.* 1986), showing that the seeds suffer lower predation. Seed burial also reduces the risk of seeds being discovered by predators or being attacked by pests. Experiments have shown that buried seeds disappear at far lower rates than seeds laid out on the soil surface (Vander Wall 1990).

4.2 FACILITATION OF ESTABLISHMENT AND GROWTH

The burying of seeds by scatterhoarding rodents facilitates seedling establishment (Forget 1990, 1997a), and is even a prerequisite for germination in some rodent-dispersed species (Vander Wall 1992). The reason is probably that the availability of water for buried seed is more stable, preventing rot during moist periods and desiccation during periods of drought (Forget 1990, Kollmann & Schill 1996). The latter is especially important for recalcitrant seed species. Furthermore, roots of buried seed penetrate the ground more easily, and emerging seedlings are rooted more firmly. An unexplored idea is that burying by rodents might stimulate interaction with (endo-) mycorrhizal fungi (Pirozynski & Malloch 1988).

An interesting hypothesis is that scatterhoarding favours seedling establishment and growth by increasing the proportion of seeds in favourable microenvironments, such as treefall gaps. Both buried seeds and seedlings of *V. americana* and *C. procera*, for instance, perform better in canopy gaps than in understorey (Forget 1997a), as do other large-seeded plant species (e.g. Kazuhiko *et al.* 1997). Scatterhoarding could, for instance, be

advantageous because a tendency of hiding seeds near objects renders a directed dispersal to light environments if such objects are correlated with canopy gaps. Logs in the forest, however, are mainly in the understorey since most canopy openings close within five years (Van der Meer & Bongers 1996a, b). Alternatively, scatterhoarding could be advantageous simply because a regular spacing of seeds increases the number of independent chances of seed hitting the patch-wise distributed canopy gaps.

4.3 THE FATE OF NON-SCATTERHOARDED SEED

Compared to the various potential benefits that scatterhoarded seeds face, the fate of seeds that remain below parent trees seems disastrous. Many studies at tropical sites have shown that seeds below parent trees suffer heavy density-dependent insect attack (Hammond & Brown 1998). Seeds of large-seeded species that were placed in batches below typical parent trees usually died (if not removed) due to predation by granivorous insects and ungulates (notably peccaries). For instance, moths had infested all *C. procera* seeds that had not been removed from experimental seed plots under adult trees after one month, (N = 20 adult trees, Paracou, French Guiana; Forget 1996). *V. americana* seeds that are not buried are attacked by insects (Curculionids) and lose their ability to germinate, especially in dry conditions (Forget 1990). Almost no *V. americana* seedlings establish when seeds are not dispersed, although some seedlings may survive in dry years (Forget 1997b).

Once seeds contain larvae, they have a lower chance of being removed and hoarded, because agoutis and acouchies avoid caching such seed with short storage lives. Peccaries, in contrast, do eat infested seed. Cafeteria experiments in which acouchies were observed foraging on mixtures of infested and uninfested seeds of *L. alba* showed that the animals are very skilled in distinguishing good and bad seeds by smell. All seeds were removed except for the infested ones (P.A. Jansen & A. Siepel, unpublished data). Furthermore, infested seeds have lower chances of germinating. In *C. procera*, for example, germination of infested seeds was 14% (N = 96 seeds; Forget 1996), while 97% of seeds free from infestation germinated (N = 182; P.A. Jansen, unpublished data). Moreover, infested seeds that do germinate should make smaller, less vigorous seedlings due to reserve consumption by insects.

Parent trees of *C. procera* along canopy gaps had quite high recruitment (from surface seeds) below them in some years, including seedlings that managed to emerge from infested seeds. This is in line with the idea that effects of invertebrate attack (of both seeds and seedlings) can be buffered by light availability, leading to establishment of seeds that would otherwise have died (Hammond & Brown 1998). Such buffering of infestation effects by light supports the idea that directional dispersal towards treefall gaps, all other factors being equal, could already make dispersal by scatterhoarders advantageous to trees.

5. Mutual benefit?

It is beyond doubt that rodents benefit from scatterhoarding tree seeds. Acouchies and agoutis actively choose to scatterhoard, because they need stored seeds to supplement their diet during a later period of food scarcity (Henry 1999). Whether scatterhoarding is also beneficial to the tree species that passively undergo scatterhoarding is far less clear. It is even questionable, since seedling recruitment conflicts with the interest of individual acouchies and agoutis.

The current idea that the relationship between scatterhoarders and trees must be mutualistic is largely based the logic that net survival below parent trees is often close to zero, so any survival must come from scatterhoarded seeds. The evidence, however, is merely circumstantial, and does not rule out alternative possibilities for regeneration, such as that establishment of non-scatterhoarded seeds occurs rarely (e.g. only in particular years), yet sufficiently often during a tree's life span. This section therefore focuses on the net benefit of scatterhoarding for the plants. We will discuss whether and how advantages for trees of having their seed scatterhoarded weigh up against the exploitation of seed supplies by the rodents.

5.1 THE FATE OF SCATTERHOARDED SEED

To determine whether scatterhoarding indeed contributes to the fitness of the parent plants we shall have to compare the probabilities of establishment between seeds that are scatterhoarded and seeds that are not. However, determining the fate of scatterhoarded seed is difficult. It requires that individual seeds be followed until they either die or establish. This is very much complicated by active management of cached seed by the rodents. It is meaningful that the net survival of seed scatterhoarded by any species has been estimated in so few studies (Vander Wall 1994, 1995a, 1995c, Vander Wall & Joyner 1998), only on short distances, and only for a limited part of the batch that was followed. Tracking seeds managed by acouchies and agoutis is particularly complicated because of the dense habitat and the large distances covered. The repeatedly surveying of large areas for protruding threadmarks of buried seeds is extremely labour-intensive. Tracing methods such as the spool-and-line method have been effective for tracking acorns dispersed by *Apodemus* mice over short distances (0.6 to 9.5 m; Yasuda *et al.* 1991), but appeared to be unsuitable for tracking seed dispersed by acouchies (personal observations). The use of transmitters (Sone & Kohno 1996) is also unpractical for following the fates of many seeds simultaneously. Consequently, the comparison of seed fates remains a major challenge in this field of research.

So far, attempts to follow naturally and artificially cached seed have shown that acouchies, agoutis and peccaries are very efficient in (re)locating cached seeds. Most naturally cached seeds disappear shortly after caching. Experiments with artificial scatterhoarding, which control for exploitation by the scatterhoarding animal itself, indicated that the chance of cached seeds being discovered by vertebrate cache thieves is very high (P.A. Jansen, R. Brienen & P.M. Forget, unpublished data). These findings, however, do not imply that survival is low, for two reasons. First, rodents are known to re-cache seeds, which may again escape consumption. Second, the high robbery risk for artificial caches may be an artefact of seed manipulation.

Planting experiments suggest that germinating seeds are even more vulnerable to predation by scatterhoarders than seeds. Scatterhoarding rodents attack establishing seedlings while managing or exploring their supplies, and seem to use emerging sprouts as cues (P.A. Jansen, unpublished data; N. Smythe, personal communication). Epigeal seedlings (e.g. Leguminosae, Meliaceae, Myristicaceae) can be uprooted or severely damaged when rodents remove the seed, while hypogeal seedlings (e.g. Sapotaceae) are usually killed as the cotyledons are eaten. If seed consumption continues till the seed is entirely and clearly empty, the net result of scatterhoarding must be estimated from the proportion of fully established seedlings.

5.2 SHORT MEMORIES AND OTHER ESCAPE ROUTES

Theoretically, rodents do best by hiding not a single seed more than they need, come back to eat every single one of them, and leave no benefits whatsoever for the plant. How then can scatterhoarding in any way be beneficial to plants? The most common line of reasoning is that seeds escape consumption simply because the animals forget caches, notably because memory capacity drops after scatterhoarding. Thus, the hoarder becomes a naive searcher for caches. While some scatterhoarders, such as Clarck's nutcracker (*Nucifraga columbiana*), remember caches for extremely long periods of time (Balda & Kamil 1992), diurnal rodents indeed tend to depend on short-term spatial memory for relocating caches (Jacobs 1992, MacDonald 1997).

Another possibility is that rodents play safe by always storing more seeds than they will probably ever need, because they are unable to predict what part of the hidden food will spoil or be stolen by food competitors, or how scarce food will be during the following season. Storing too few seeds is lethal and, therefore, strongly selected against. If animals habitually store food in excess, part of their supplies will normally be left and may eventually germinate and establish.

Lastly, a high population turnover of rodents may help seeds to escape consumption no matter the efficiency of rodents in depleting their caches. Both acouchies and agoutis are short-lived and are important prey for many raptorial animals. From one year to the next, Dubost (1988) recovered only five out of 16 marked agoutis at the same site (42% site fidelity), four at new sites, while the remaining seven were not recovered. Of 22 marked acouchies Dubost recovered none at all (0% site fidelity). This indicates that territories may frequently get vacant, and that the chances of a rodent not depleting its hoards could therefore be high. A logical mechanism is that seeds escape consumption because the animal dies before the depletion of its reserves. Seeds escaping consumption because the animal abandons its territory and reserves seems not logical, given the strong dependence of these rodents on stored seed.

The way in which seeds escape consumption should be visible in the spatial pattern of seedling recruitment. If seed survival and plant reproductive success were determined by loss of memory or structural excess storage, scatterhoarding would yield seedlings everywhere in every year. If, in contrast, local population fluctuations (due to death and migration) or variation in seasonal food availability determined seed survival, scatterhoarding would only yield seedlings once in several years. And if seed survival mainly depended on mortality of the individual scatterhoarder, seedling recruitment would be cohort- and territory-wise. The loss of seed crops in a number of years would then be the price paid for one successful crop.

6. Evolutionary aspects

The interactions between scatterhoarding rodents and large-seeded trees have some interesting evolutionary aspects. If the net effect of scatterhoarding for plants were negative, plants would be expected to have evolved mechanisms discouraging scatterhoarding. Instead, examples of plants exist that seem to have done the opposite; their fruit composition, seed size and phenology rather promote scatterhoarding (Vander Wall 1990). Given the large proportion of seeds affected by scatterhoarding in these plants, the reasoning that scatterhoarding must be beneficial and that plants are adapted to it is

tempting. This has given rise to claims of coevolution of plants with scatterhoarders, for instance of pinion pines with chipmunks (Vander Wall 1993b), and of black walnut with fox squirrels (Stapanian & Smith 1986). However, it is impossible to prove that plants have evolved in response to interaction with scatterhoarders. What can be done, however, is measuring direction and strength of selective pressures that scatterhoarding and other factors impose on the reproductive strategies of these plants.

6.1 STIMULATING SCATTERHOARDING

The driving force behind a mutualistic interaction should be sought in the common interest of plants and rodents in preventing other granivorous insects and mammals to consume seed. The continuous threat of seeds being infested by insects or eaten by peccaries, thus becoming unattractive or unavailable for scatterhoarding, makes it important for plants to minimise the time that elapses between seed shedding and the moment at which a rodent removes the seed.

Theoretically, there are several possible ways by which plants could increase the speed and proportion of seeds being scatterhoarded. Individual plants that produce seeds in a way that is more attractive to scatterhoarding rodents could have their seeds scatterhoarded in larger numbers and more quickly than other individuals. Consequently, such individuals may be presented more heavily in future generations than others of the same species (Smith & Reichman 1984, Vander Wall 1990). Producing a greater number of seeds at a time, for example, could increase the chances of rodents finding the seed source, and starting to frequent it for exploitation. However, the high rate at which laid-out batches of seeds (simulating new seed sources) are discovered by acouchies and agoutis has convinced us that the number of seeds available at a time is of only limited importance for discovery.

In contrast, the nutritional value of individual seeds appears all the more important. Removal rates of seed species with different characteristics differ enormously. If plants producing high-valued seeds are frequented with greater fidelity than plants with less valuable seeds, producing more nutritious seeds with longer storage life may be rewarded with reduced exposure time to insects and wild pigs, i.e. reduced seed predation below the parent plant. Rodents also tend to hide valuable seeds more carefully than food of lower value (Stapanian & Smith 1986). Accordingly, larger seed tend to be transported further and spaced apart wider than smaller seeds (Stapanian & Smith 1984, Forget *et al.* 1998), which might yield survival advantages. The idea that strong competition for rodents between individuals and/or superior treatment of higher-valued seeds might have lead to frequency-dependent selection for ever-larger and more nutritious seeds is an intriguing explanation for the prevalence of large seeds among plants dispersed by scatterhoarders (Vander Wall 1990, Andersson & Frost 1996).

Plants could also influence the proportion of seeds surviving by fruiting when rodents are more likely to scatterhoard seeds. For instance, the proportion of seeds scatterhoarded increases during the wet season for both *C. procera* (Forget 1996) and *V. americana* (Forget 1990). When an individual tree sheds seed late, while seeds shed later are removed more quickly, its seeds could have short-term survival advantages. A general pattern is that plant species potentially dispersed by scatterhoarding rodents tend to mature during one specific season. Jackson (1981) found that seed fall of large-seeded species in a Brazilian lower montane moist forest peaked in the wet season, whereas small-seeded species were much less seasonal. In French Guiana, large-seeded species also tend to fruit more or less

synchronically in the wet season. Could this have to do with the fact that rodents scatterhoard more in this season than in any other? Or can the synchronous fruiting be explained by reduction of predation risk because predators are satiated? Smythe (1970) has suggested such selection of scatterhoarding rodents on the fructification of large-seeded plant species.

Fruiting phenology may also influence rates of scatterhoarding. The phenologies of rodent-dispersed species vary considerably. *V. americana* sheds numerous seeds within a period of only two or three weeks, once every few years. *C. procera* seed shedding, in contrast, is modest, spreads out over two months, and occurs nearly every year (Forget 1997a). The advantage of peaked production could be that it causes satiation, and stimulates rodents to hoard the excess of seeds. The implicit idea is that the rodents will eat a greater proportion of the seed if they have the appetite. Spreading production, alternatively, may be more in pace with the rate at which animals are able to store seeds, and could reduce the duration of seeds lying waiting to be hoarded. This strategy demands a motivation of the rodent to store seeds independent of appetite, for instance, because of certain compounds that hamper instant digestion but lengthen storage life.

Given that there are limits to the amount of nutrients a plant can allocate to reproduction, plants face a trade-off between producing more nutritious seed and producing many seed. However, it might be essential to produce seed in large numbers that are nutritious at the same time. From this perspective, the phenomenon of mast fruiting may be a way for rodent-dispersed plants to escape from this limitation, by saving up energy during few years by not fruiting, in order to enable a more abundant fruiting in one subsequent year. According to the 'disperser attraction hypothesis' (Barnett 1977), the function of abundant fruiting is to attract seed dispersers, according to the 'predator satiation hypothesis' (Janzen 1971), the function is to satiate seed predators. These hypotheses are in fact complementary, with the former stressing the positive role and the latter stressing the negative role of animals. Since scatterhoarding rodents play both roles, both hypotheses may hold for the mast fruiters that have their seed scatterhoarded.

6.2 MONOPOLISING SEED RESERVES

Ultimately, provisioning and dispersal conflict. The interests of rodents and plants become completely opposite when it comes to exploitation of stored seed by the scatterhoarder. Seedlings and rodents are in competition for the seed reserves. What ways might plants have to minimise damage due to cache exploitation?

The most obvious way for plants to anticipate cache exploitation by rodents is through their timing and rate of germination. Certain plant species, such as *C. procera* and *V. americana*, start establishing before the animal actually starts drawing upon its seed supplies. The high mortality risk of establishing plants due to fungi in the wettest months and due to drought in the driest months (Forget 1997a) may also be avoided in this way. Repeated inspection and management of seed supplies by the rodents, however, severely limits the chance of seedlings emerging unnoticed, especially when shoots are used as cues. When digging up the seed, the rodents often damage or uproot the seedling.

It may be useful for seedlings to speed up establishment and the transfer of seed reserves into the seedling. The vulnerable phase of emergence can be rapid, and set on when rooting and transferring seed reserves to roots are already well on their way. Other than avoiding damage to the shoot, plants can also mitigate rodent-induced damage (e.g.

shoot cutting). Large seed reserves, transferred to the seedling, may function as a risk hedge (e.g. Kazuhiko *et al.* 1997). This advantage of large seeds combines well with having large seeds to stimulate scatterhoarding.

   An alternative strategy, avoiding a race for seed reserves, may be to delay germination till the next period of food abundance, when no rodent will be managing old seed reserves. *L. alba* and *Astrocaryum* may do this. Delayed germination requires increasing seed storage life, which happens to be attractive for scatterhoarding rodents as well. Dispersability and seed survival may thus go hand in hand all the way to establishment.