SCATTERHOARDING AND TREE REGENERATION

ECOLOGY OF NUT DISPERSAL IN A NEOTROPICAL RAINFOREST

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SCATTERHOARDING AND TREE REGENERATION

ECOLOGY OF NUT DISPERSAL IN A NEOTROPICAL RAINFOREST

Patrick A. Jansen

Proefschrift

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Errata

Chapter 6 contains the following errors:

The figures on pages 74-75 do not correspond with TABLE 6.2, because five 1998-plots are not included. Thus,
p74: The total number of plots should be 92, not 87
p75: “2,654 seeds over 4 years“ should be “2,899 seeds over 5 years”
p75: “75 plots (2,354 seeds)” should read “80 plots (2,599 seeds)”

p84: “FIGURE 6.1A” should be “FIGURE 6.2A”

p90: The fourth line from below should read:
“... greater in poor years (74%) than in rich years (21%)

Stellingen

behorende bij het proefschrift van Patrick A. Jansen,
"Scatterhoarding and tree regeneration. Ecology of nut dispersal in a Neotropical rainforest", te verdedigen op 7 februari 2003

1. Zaadetende dieren kunnen zorgen voor effectieve zaadverspreiding, zelfs al eten zij het overgrote deel van de zaden op.
   Dit proefschrift

2. Terwijl pure zaadpredatoren zorgen voor selectie tegen grote zaden, veroorzaken hamsterende zaadeters juist stabiliserende selectie vóór dergelijke zaden.
   Dit proefschrift

3. Het fenomeen van mast bij nootdragende plantensoorten is te verklaren vanuit uitsluitend het gedrag van hamsterende zaadeters.
   Dit proefschrift

4. Zaadverspreidende dieren vormen een belangrijk element van bosbeheersystemen op basis van natuurlijke regeneratie, en moeten daarom worden beschermd.
   Dit proefschrift
   P.D. Moore, 2001. *Nature* **409**: 775 – 777
   C.A. Peres, 2001. *Conservation Biology* **15**: 1490-1505

5. Dat bloemrijke wegbermen steeds belangrijker worden voor de Nederlandse biodiversiteit is een gevaarlijke ontwikkeling, niet iets om alleen maar trots op te zijn.

6. Een baby is geen larf, laat staan de beste larf die er op de wereld bestaat.
   vergelijk M. Dekkers, 2002. *De larf.* Uitgeverij Contact, Amsterdam

7. Het goede is de vijand van het betere.

Voor mijn ouders en voor Kristel

Abstract

Jansen, P.A. (2003) Scatterhoarding and tree regeneration. Ecology of nut dispersal in a Neotropical rainforest. PhD thesis, Wageningen University, Wageningen, the Netherlands. ISBN 90-5808-777-8; x + 166 pp.

Seed-eating animals are reputed predators of seeds, but they may also function as seed dispersers. This dissertation deals with the interaction of nut-bearing trees and scatterhoarding animals, which store important amounts of seeds as food reserves in spatially scattered soil surface caches. It studies how large cavi-like rodents – in particular the Red acouchy – disperse and predate upon the seeds of the canopy tree *Carapa procera* (Meliaceae) at the Nouragues Biological Station, an undisturbed tropical rainforest site in French Guiana, South America. *Video surveillance and thread-marking techniques* were used to follow the fate of seeds throughout the dispersal process, from shedding until either death or establishment of a seedling. Thus, seed production was linked with dispersal effectiveness and establishment success. Within these seed fate experiments, seed size and seed abundance were varied to study how these plant traits affect scatterhoarding and to test hypotheses on the evolution of large-seediness and mast seeding.

Scatterhoarding proved to be an effective dispersal mode. Seedlings did establish from cached seeds, even though the majority of seeds were eventually dug up and consumed. Large seeds were more likely to be successfully dispersed than small seeds, which opposes the paradigm that the need for dispersal causes selection against large seeds. Large seeds, however, were favoured only up to a certain point beyond which seeds apparently became increasingly difficult for the animals to manipulate. This resulted in an optimum seed size for dispersal by scatterhoarding animals. An explanation is given for the contrasting results obtained in published experiments on size-dependent seed predation.

Establishment was far more likely in years of abundant fruiting than in lean years, and the selectivity of rodents regarding the size of scatterhoarded seeds was also greater in rich years. Scatterhoarder responses to seed size and abundance alone can explain why many nut-bearing plant species have mast seeding, the alternation of years with abundant crops and years with few or no seeds.

Regeneration of *C. procera* in natural forest came exclusively from seeds cached by scatterhoarding rodents: seed predating insects and mammals destroyed all non-dispersed seeds. Exceptions were seeds shed by parent trees along or within treefall gaps. These high light environments permitted seedling establishment even from heavily infested seeds. Therefore, regeneration need not be at immediate risk in managed forests where scatterhoarding rodents are scarcer, but where light availability tends to be greater.

Key-words: scatterhoarding rodents, natural regeneration, seed dispersal, seed predation, seed size, mast seeding, natural selection, *Myoprocta exilis*, *Carapa procera*, Meliaceae

Contents

Voorwoord

Onderzoek doen in tropisch regenbos is een droom die vele veldbiologen koesteren. Ook ik deed dat, en met dit promotie-onderzoek is die droom gerealiseerd. Ik mocht werken op een geweldige plek – het ongestoorde regenbos van Nouragues in tropisch Frans Guyana. Een plek die ik liefheb vanwege de natuur en tegelijkertijd haat vanwege de maandenlange afzondering van thuis en de eenzame opsluiting in een kleine groep mensen waarmee het toevallig maar moet klikken. *Je remercie Pierre Charles-Dominique et le Centre National de Recherche Scientifique pour me permettre de travailler aux Nouragues.*

Zes jaar lang heb ik in Frans Guyana en Wageningen kunnen doen waar ik zin in had, onderzocht ik wat ik zelf had uitgedokterd en waarvoor ik zelf de financiering had gezocht. Helemaal vrij zijn om te onderzoeken waar je nieuwsgierig naar bent, als het maar leidt tot een proefschrift: dat is een ongekende luxe. Dank aan de Nederlandse Organisatie voor Wetenschappelijk Onderzoek, die brood zag in mijn ideeën en plannen, en geld overhad voor de uitwerking ervan.

Ik ben dan ook niet alleen maar blij dat het af is. Want het is nog helemaal niet af. Er liggen nog zoveel gegevens te wachten om geanalyseerd te worden en verhalen over te schrijven, zoveel vragen om te beantwoorden, zoveel ideeën om te toetsen aan de werkelijkheid, en zoveel onuitgevoerde plannen. Ik zou mijn hele leven wel willen promoveren. Maar dan wel zonder de tijdsdruk die met name de afgelopen anderhalf jaar mijn privé-leven zo sterk beïnvloedde en alle vrije tijd opslokte. Ik hoop dat resultaat de moeite waard zal blijken.

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I am honoured that Pierre-Michel Forget is willing to be a member of the committee. The subject of this thesis came from stimulating discussions with him, and his impressive publications and unique expertise were an invaluable foundation for my fieldwork. I hope that I have not been poaching on his territory too much, and I look forward to further co-operation.

Bijzonder tevreden ben ik ook met de verdere samenstelling van de promotiecommissie. Jan van Groenendael was een prima begeleider van mijn opleidingsprogramma, al vermoed ik dat hij niet zal begrijpen waarom ik dat vind. Ik bewonder zijn werk en ben er trots op dat hij nu deel uitmaakt van de commissie. Ook Louise Vet mocht zeker niet ontbreken in de commissie. Zij heeft de afgelopen jaren voortdurend belangstelling getoond voor mij en mijn werk en me telkens weer uitgedaagd om nieuwe stappen te zetten in de wetenschap. Ik heb groot respect voor haar. Jacques van Alphen, tenslotte, was degene die me liet gaan toen mijn onderzoeksvoorstel door NWO werd goedgekeurd. Ik denk nog vaak over hoe het zou zijn geweest om voor hem met Kristel naar Panama te zijn gegaan, in plaats van alleen naar Frans Guyana. Het doet me plezier dat Jacques, die mijn project de afgelopen jaren voortdurend volgde, wil opponeren.

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Mijn tijd in Wageningen heb ik vooral achter het bureau doorgebracht bij Bosbouw, waar ik vier pc's versleet. Vooral Villa Hinkeloord was een geweldige werkplek: een eigen kamer met uitzicht op het Arboretum, waar je de eekhoorns zwarte walnoten zag hamsteren en Vlaamse gaaien de eikels. Met mijn vrienden en collega-promovendi bij Bosbouw – Michiel van Breugel, Mirjam Kuzee, Peter van der Meer, Marc Parren, Lourens Poorter (eigenlijk Utrecht, maar wat geeft dat), Toon Rijkers, Frank Sterck en bovenal Jan den Ouden – heb ik veel plezier gehad en gefilosofeerd over spannend onderzoek, de ultieme analyse, de organisatie van de vakgroep, en over hoe het onderwijs eruit zou moeten zien. Hun gedachten over mijn onderzoek, de presentaties en de manuscripten waren van grote waarde. Het doet me veel plezier dat Jan paranimf wil zijn bij de verdediging van dit proefschrift.

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Patrick Jansen,
31 december 2002

1. General introduction

The dispersal phase is one of the most critical in plant life history. It involves the greatest losses of individuals, both absolutely and relatively, as only very few or even none of millions of seeds that individual plants may produce during their lifetime will successfully establish and become reproductive. But it also involves great challenges to plants. By relatively successful dispersal, individuals or species can pass a disproportionate amount of genes to the next generation. Dispersal failure, on the other hand, can completely eradicate an individual's or species' representation in the next generation. Dispersal therefore has a profound effect on vegetation composition and even structure (Wang and Smith 2002).

Although recent studies have taken away all doubt about the importance of seed dispersal for plant demography and biodiversity, our knowledge of how seed dispersal works and what it implies for plant reproductive strategies is still poor. The three main reasons are that seed dispersal in most cases is a very complex process, highly variable in time and space, and notoriously difficult to follow (Wang and Smith 2002). This holds especially for seed dispersal by animals, which is the dominant dispersal mode in many tropical forests. Studies of animal-mediated seed dispersal have usually been too short, were unsuccessful or incomplete in tracking seeds, or considered too small cohorts to link seed production and plant reproductive success. My study of animal-mediated seed dispersal is an attempt to link seed production and seedling recruitment by avoiding these limitations.

1.1 Dispersal by scatterhoarding

Plants have evolved an incredible diversity of mechanisms to have their seeds dispersed (Van der Pijl 1982). Adaptations include plumes and wings to have seeds carried away by the wind, hooks and spines to get seeds attached to animal fir, air cavities on which seeds can drift to far horizons, and palatable fruit pulp to persuade vertebrates swallowing seeds. Dispersal by scatterhoarding animals is peculiar in that the seeds themselves, rather than their envelopes, are the food rewards that persuade animals to disperse them. The seeds are typically large, nutritious nuts, that scatterhoarding animals harvest and bury in numerous spatially scattered caches in the soil surface. The animals create these food supplies to anticipate periods of seed scarcity, such as winters in the Temperate Zone (Wauters *et al.* 1995) and the dry season in many tropical forests (Henry 1999). Most of the seeds are therefore recovered and eaten, but some are left to germinate and establish seedlings.

It is believed that seed handling by scatterhoarding animals tends to be beneficial to plants. The long-term perspectives of the cached seeds escaping would outweigh the costs of the many other seeds that are eaten. This is also suggested by seed characteristics that encourage rather than discourage scatterhoarding, such as large size, high nutritional value, and low chemical and physical defence. Nonetheless, the role of scatterhoarding animals as potential seed dispersers has long been ignored. Even today, seed removal by scatterhoarders is often equalled to seed predation. One of the reasons is that only a handful of published studies have actually been able to track scatterhoarded seeds and determine their ultimate fate, and none of these were in tropical forest (Chambers and Macmahon 1994).

The interaction of plants and scatterhoarding animals, which are seed dispersers and predators at the same time, has several interesting evolutionary aspects. Smith and Reichman (1984) have hypothesised that the production of large, nutritious seeds by nut-bearing plant species has evolved in response to feeding preferences of scatterhoarding animals. The idea behind this 'seed size selection hypothesis' is that the animals will select the seeds with the highest nutritional value for scatterhoarding, and will ignore or eat the remaining seeds. Many nut-bearing plant species also tend to produce large seed crops at intervals of two to five years, with large and small nut crops differing in size by 2 or 3 orders of magnitude Vander Wall (2001). An important explanation for this phenomenon, called mast seeding, is the 'predator satiation hypothesis' (Janzen 1970, 1974; Silvertown 1982). It proposes that mast seeding is an evolutionary response to intense seed predation. The idea is that trees, by producing huge crops in some years, swamp seedeaters with food and allow seeds to escape predation and successfully establish, while low seed crops in the intermittent years may prevent seedeaters from adapting their population levels. In case of scatterhoarding animals, the function of mast seeding would be to stimulate scatterhoarding seedeaters acting more as dispersers and less as predators of the seeds they harvest.

1.2 This study

My work had three goals. First, I wanted to find out whether large seeds disappearing from the forest floor were indeed removed by scatterhoarding animals, and whether these seeds had some chance of survival. This is related to the ecological question of how important seed dispersal by scatterhoarding animals is. Secondly, I wanted to know to what extent large-seeded tree species depend on scatterhoarding for regeneration. This is related to the practical question whether forest management systems should involve the strict protection of scatterhoarding animals. Presently, seed dispersing animals tend to be forgotten in forest management, while at the same time management systems increasingly rely on natural regeneration. This might be unsustainable. Webb and Peart (2001), for example, predicted that removal of animal dispersers would reduce seedling richness by as much as 60%. Thirdly, I wanted to know whether scatterhoarding animals caused a selective pressure on plant reproductive traits, seed mass and mast seeding in particular. This is related to the evolutionary question whether large seeds and mast seeding may have evolved in response to selection by scatterhoarding animals.

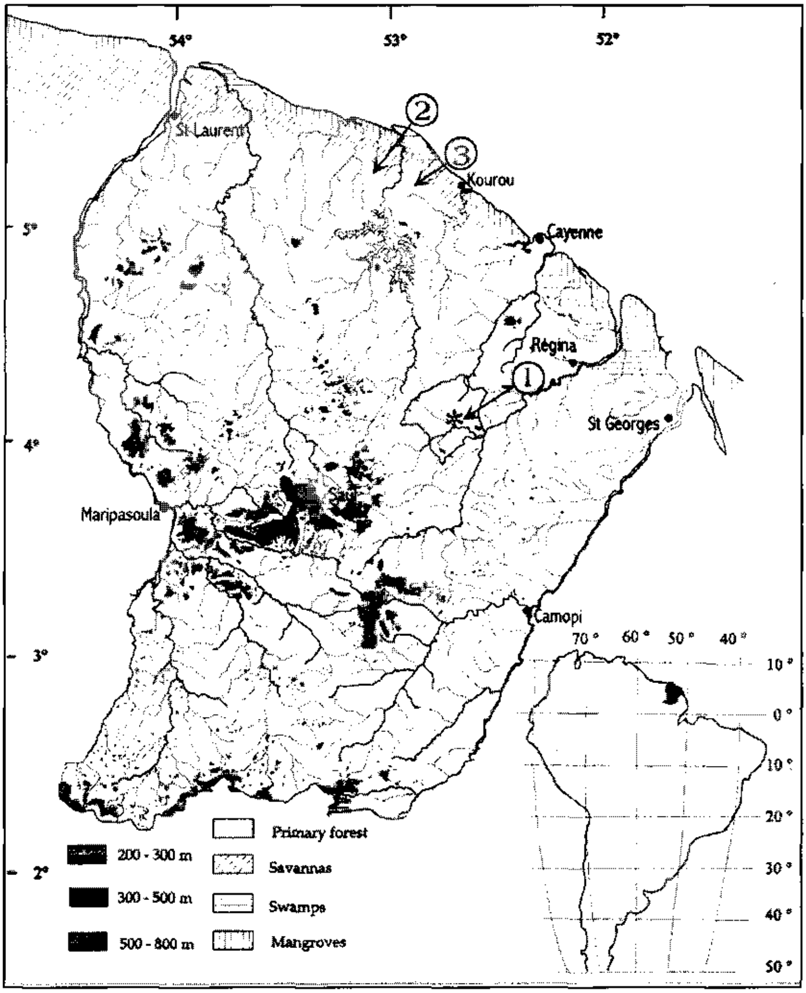

Figure 1.1 Location of the study site – Nouragues Biological Station, indicated by number 1 – in French Guiana and South America. Numbers 2 and 3 indicate Piste de St. Elie and Paracou, respectively, two other Guianan field stations. From Bongers *et al.* (2001).

My study species were Neotropical nut-bearing trees whose seeds are scatterhoarded by large terrestrial rodents. They were ideal for my study, because dispersal is relatively simple and easy to document. The seeds can easily be marked and tracked individually because they are large and not embedded in fruit pulp. Also, the seeds need not be marked and tracked in the canopy, because all dispersal is áfter seed shedding. Moreover, the rodents have no cheek pouches and handle seeds individually, one by one. This makes that handling can be coupled to the properties of individual seeds. Finally, the rodents usually hide seeds in the soil surface rather than taking them up into trees or into burrows where we cannot track them.

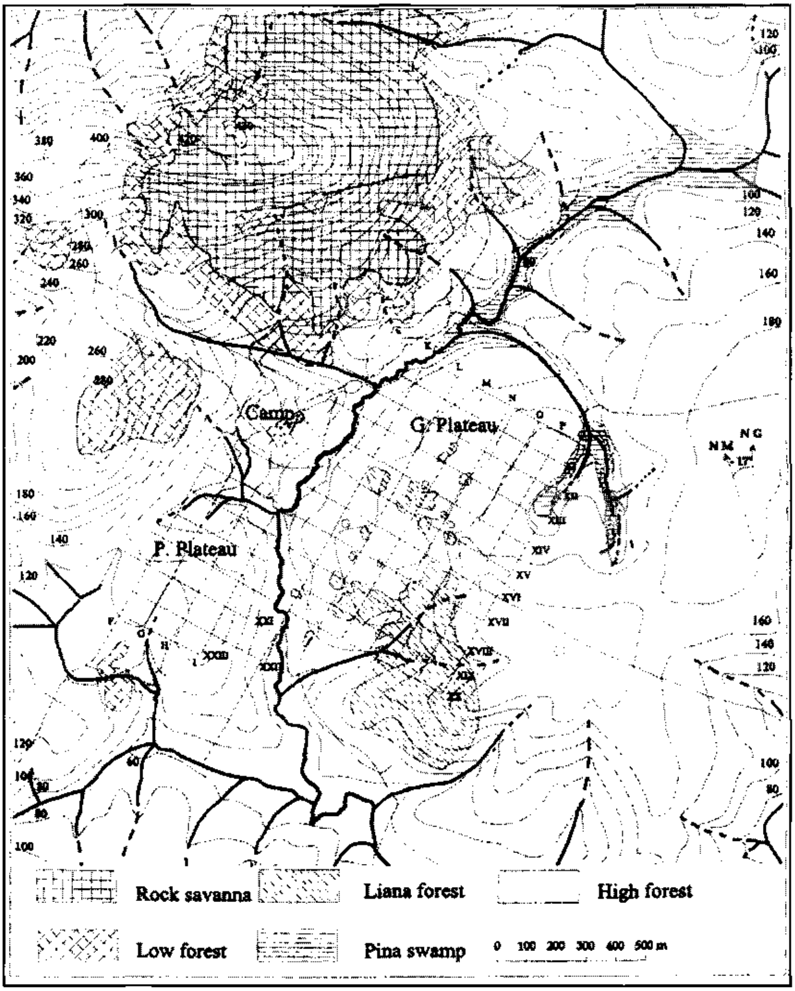

Figure 1.2 Map of the study area. The grid lines indicate the trail system enclosing 1ha-quadrats of the tree cartography. Topography is indicated by 20m-interval isoclines. From Bongers *et al.* (2001)

1.3 Site

The experiments reported in this dissertation were all carried out at the Nouragues Biological Station in French Guiana, South America. This field station, established 1986, is located about 100km south of the city of Cayenne, at 4°05'N and 52°40W (FIGURE 1.1). The station is in the centre of the Nouragues rainforest reserve at the base of a 430m high inselberg. The local forest is pristine (PHOTO 1.1). Human impact dates from before the early 19th century, when the Nouragues native Amerindians left the area (Charles-Dominique 2001). Annual rainfall averages 2,990mm. Most rainfall (>250mm mo^{-1}) occurs in January-June, the rainy season, and minimum rainfall (<100mm mo^{-1}) during September-October (Grimaldi and Riéra 2001).

Photo 1.1 Aerial view of high mature forest at Nouragues, French Guiana

I chose to do my fieldwork at the Nouragues site for several reasons. First, nut-bearing trees occur in fairly low densities (several individuals per ha) in these forests, with reproductive individuals spaced apart. This makes it easier to distinguish seedlings that have established below and away from their parent. Secondly, the pristine conditions at Nouragues allow studying scatterhoarding under natural circumstances, which is as close as one can get to the conditions under which this plant-animal interaction evolved. Thirdly, many previous studies on scatterhoarding had been done at this site (Forget 1990, 1991a, 1991b, 1992, 1994, 1996). These provided a sound foundation for my work. An extensive description of the Nouragues site and research carried out there can be found in Bongers *et al.* (2001).

All experiments were carried out in high mature forest, mostly within the ongoing 100ha cartography in which trees beyond 10 or 30cm dbh, depending on the site, have been measured and mapped (FIGURE 1.2). This forest has tree densities ranging from 468 to 681 stems (≥10cm) dbh per ha, and a fairly open understorey (Poncy *et al.* 2001). 550 tree species from 63 families have been identified (Belbenoit *et al.* 2001). The most important families are the Caesalpiniaceae, Sapotaceae and Lecythidaceae. The two sites distinguished in this thesis differ strongly in soil. The so-called 'Petit Plateau' is a *ca.* 30ha hilltop at the foot of the inselberg with shallow soils on granitic rock. These are very poor, highly acidic, and poorly drained cambisols-ferralsols. The so-called 'Grand Plateau' is the shallow slope of a more than 5km^2 plateau with deep, clayey, less acidic and well-drained ferralsols (Grimaldi and Riéra 2001). Plants at the Petit Plateau are more likely to suffer drought stress than plants at the Grand Plateau.

Photo 1.2 The composed fruits, husks and seeds of the study species, *Carapa procera*. The diameter of a fruit is approximately 10cm.

1.4 Species

I used several tree species for my experiments. The most important were *Carapa procera* D.C. 1824 (Meliaceae), *Vouacapoua americana* Aubl. 1775 (Caesalpiniaceae) and *Licania alba* (Bernoulli) Cuatrec 1964 (Chrysobalanaceae). These tree species are among the 75 largest at Nouragues, attaining diameters greater than 70cm and heights greater than 40m. All are hard-fruited with large nuts (>15g average fresh seed mass), that are harvested and buried by two scatterhoarding rodents, Red acouchy (*Myoprocta acouchy*, Erxleben 1777) and Red-rumped agouti (*Dasyprocta leporina*, L. 1758), and attacked by peccaries and various insects. The seeds have epigeal germination, which means that the seedling emerges while the nut remains buried (Garwood 1996).

The species differ in their supra-annual fruiting rhythm: while *V. americana* and *L. alba* show synchronous fruiting once every 2-4 years (mast seeding), *C. procera* sets fruit annually. The seeds also differ in their vulnerability to insect predation and in chemical composition, and in germination speed. While *V. americana* and *C. procera* have soft-shelled recalcitrant seeds (Connor *et al.* 1998) that germinate within few days or weeks after shedding, *L. alba* has hard-shelled seeds that take a full year to germinate.

Especially *C. procera* (PHOTO 1.2) played an important role in my experiments. The 20-fold variation in seed mass within this species' population allowed studying the effect of seed size while controlling for other seed variables. This means that the results are not complicated by confounding variables such as seed chemical composition, physical protection, and perishability that likely affect animal preferences (Hurly and Robertson 1987), as in the alternative approach: a comparative study with different-sized seed species. Moreover, the fact that *C. procera* seed was available every year, albeit in greatly varying quantities, allowed comparing dispersal of a single seed species against a varying background food availability. This made *C. procera* an ideal model species for my evolutionary questions.

The two species of scatterhoarders involved are both cavimorph rodents: the Red-rumped agouti (*Dasyprocta leporina*, L. 1758) and the lesser-known Red acouchy (*Myoprocta acouchy*, Erxleben 1777) (PHOTO 1.3). Acouchies measure 17-20cm shoulder height and weigh 1.0-1.5kg, whereas the larger agoutis measure 26-32cm shoulder height and weigh 4.0-5.9kg (Dubost 1988). Acouchies have far smaller home ranges than agoutis and are more common at the Nouragues area. Both species are diurnal with peak activity in the early morning and in the late afternoon. They scatterhoard a variety of large seeds in a comparable way. Agoutis, and probably acouchies as well, strongly depend on cached seeds during the lean dry season (Henry 1999). Both species are affected by forest exploitation; acouchies are sensitive to habitat disturbance (Dubost 1988), while agoutis are subject to intense hunting in areas accessible to people (Ojasti 1996).

1.5 Experiments

My core experiment involved the tracking of thousands of individual seeds in time and space to determine their ultimate position and fate. During five consecutive years, I placed individually marked seeds in experimental feeding plots and used video surveillance cameras to monitor how animals removed them. I then searched the surrounding area to retrieve seeds, threadmarks protruding from the soil giving away the hide of cached seeds. Subsequently, I tried to follow the cached seeds until they had either died or established. I also examined whether scatterhoarding brought seeds into favourable places, away from adult trees and towards treefall gaps.

The results enabled me to evaluate whether scatterhoarding rodents indeed were effective seed dispersers or simply seed predators (QUESTION 1), and to determine whether the trees are depending on scatterhoarding for regeneration (QUESTION 2). Within the seed fate experiments, I varied seed size, while seed abundance varied between years. This enabled me to test whether larger seeds received a more favourable treatment than small seeds, and whether more seedlings emerged under seed abundance than under seed scarcity (QUESTION 3).

Several supplementary experiments and samplings are not presented in this thesis, but some results are briefly mentioned in the synthesis. These include a series of field experiments on the survival of seed caches, in which seeds were experimentally hidden under different caching strategies. Furthermore, there were experiments on the effect of distance-to-adult and light availability on seed and seedling survival, a sampling of seed and fruit production by different individuals in the population of three tree species during several subsequent years, and a comparative study of dispersal syndromes. In Wageningen, there were two greenhouse studies on the effect on seed mass on seedling vigour and the ability to recover from inflicted damage.

Photo 1.3 An acouchy, in this case the Green Acouchy (*Myoprocta pratti*), manipulating a fruit before caching the seed.

Finally, field experiments on the survival of experimental seed caches and on scatterhoarding of acorns (*Quercus robur*) by Woodmice (*Apodemus sylvaticus*) were carried out at the Veluwe, the Netherlands. These studies will be published at other occasions.

1.6 Thesis outline

The main perspective throughout this dissertation is that of the plant whose reproductive outcome depends on seed dispersal by scatterhoarding rodents and seed predation by an array of animals including the same rodents. It would also have been possible to write this thesis from the perspective of the animal whose scatterhoarding decisions determine whether is can store and maintain enough seed reserves to survive the lean dry season. The choice for the plant perspective originates from the project's proposal. It implies that the animal behavioural ecology (including feeding decisions, optimal cache spacing, cache management and cache robbery) are beyond the scope of this work. The shadow of animal behavioural ecology, however, is visible throughout the thesis. The chapters have been written for publication as papers, and can be read independently from each other. Overlap, especially in the introduction and methods sections, was therefore unavoidable.

I start with two introductory reviews. The first, CHAPTER 2, is a general review about seed dispersal in rainforest ecosystems and on the potential effects of logging on dispersal success and, ultimately, natural regeneration. CHAPTER 3 then introduces the dispersal system studied in this thesis with a review of seed dispersal by scatterhoarding animals, and many examples from three nut-bearing tree species in Guianan rainforest. This chapter explains what scatterhoarding is, why it is important for animals, and why it is though to be important for certain plant species, especially for large-seeded trees. It aims to present a state-of-the-art, identifying the lacunas in present knowledge and outlining some hypotheses that need to be tested.

The remainder of this thesis is devoted to actually answering the three main questions, and to testing some other plant-centred hypotheses introduced in chapter 3, using one of the three tree species, *C. procera*, whose seeds are much sought after by scatterhoarding rodents. CHAPTER 4 asks the question of why scatterhoarding rodents would be interested in hiding these seeds at all. Rapid seed germination characteristic for *C. procera* depletes seed reserves well before the rodents need them.

The next three papers present results from the seed fate tracking experiments that were carried out with *C. procera*. All are about the consequences of rodent feeding preferences for seed predation, dispersal and, ultimately, seedling establishment. CHAPTER 5 is a test of the major assumption underlying the idea that large-seediness has evolved in response to selection by scatterhoarding animals. I investigated whether large seeds receive a more favourable treatment by scatterhoarding rodents than small ones. Video cameras and threadmarks were used to follow the fate of seeds that greatly varied in seed mass, and determine their dispersal distances and probabilities of seedling establishment.

CHAPTER 6 is a test of the predator satiation hypothesis of mast seeding, in particular the idea that massive fruiting overwhelms seed predators so seed survival is high compared to survival in years of modest fruiting. I compared rates of scatterhoarding and cache exploitation, and the probabilities of seedling establishment between three years of low fruiting and two of abundant fruiting. It also tests the hypothesis emerging from CHAPTER 5 that seed mass affects dispersal more strongly in rich years than in poor years.

The two previous chapters tested the idea that the scatterhoarding behaviour of rodents would favour larger seeds. Reasoning that there must be a seed mass or size beyond which rodents can no longer carry seeds, CHAPTER 7 tests whether scatterhoarding acouchies favour some intermediate seed size rather than ever-larger seeds.

CHAPTER 8 considers the result of dispersal, the spatial pattern of successfully established seedlings. Seed shadows and seedling distributions of three nut-bearing tree species, as introduced in CHAPTER 3, differing in effectiveness of scatterhoarding, are compared. It is shown that the poorly dispersed species have less seedling recruitment near parent trees than expected from random recruitment from the seed shadow, while the best-dispersed species does not. Contrary to the expectations, none of the species is more common near and in light gaps.

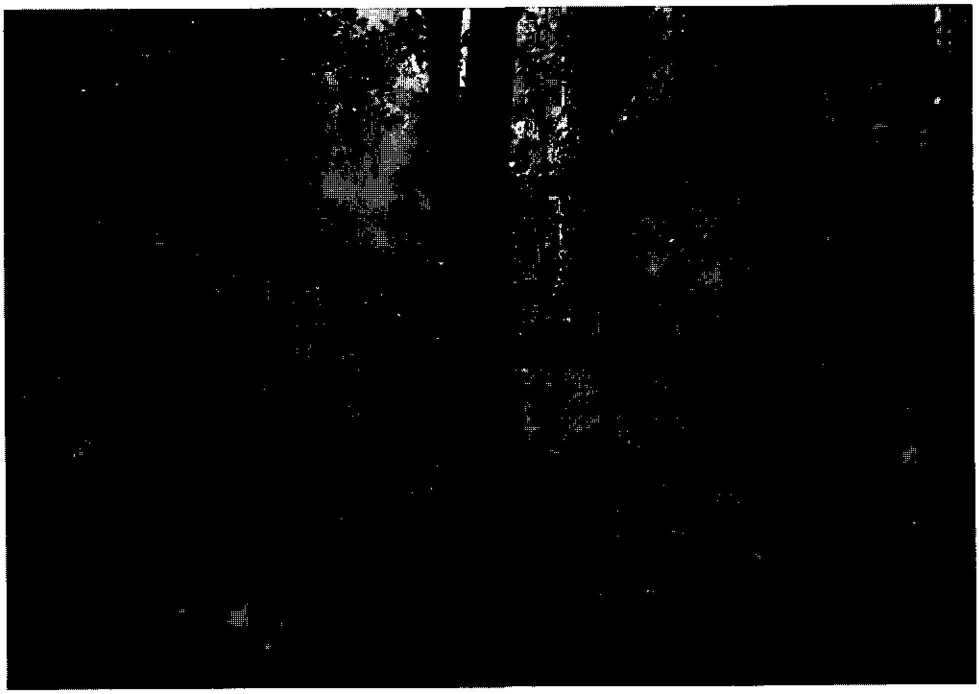

Photo 1.4 Typical dense understorey at the Nouragues field station. This is the primary habitat of the Red acouchy (*Myoprcta exilis*).

Finally, CHAPTER 9 is a synthesis of the findings, also including some results of unpublished experiments. I evaluate whether scatterhoarding rodents indeed were effective seed dispersers or simply seed predators (QUESTION 1), whether nut-bearing trees depend on scatterhoarding for regeneration (QUESTION 2), and whether scatterhoarding is more effective for large seeds and under seed abundance (QUESTION 3). Moreover, I put these results into a theoretical perspective, and propose some alternative explanations. I also indicate some directions for future research.

2. Logging, seed dispersal by vertebrates, and natural regeneration of tropical timber trees

2.1 Introduction

Tropical forestry is increasingly focused on finding systems for sustainable timber harvesting from natural forests. So-called 'natural regeneration systems' are typically polycyclic, selective logging systems that rely on natural regeneration to produce the next crop of timber (Gómez-Pompa and Burley 1991). These systems seek to maintain commercial productivity of logged forests by minimizing damage to residual trees and by conserving the natural regeneration potential of the forest (Grieser Johns 1997). Some, such as the CELOS silvicultural system (Centrum voor Landbouwkundig Onderzoek in Suriname; De Graaf 1986; De Graaf and Poels 1990; De Graaf *et al.* 1999), also include procedures to enhance regrowth of high value species by applying 'liberation' thinnings and other 'intermediate' practices (Putz *et al.* 2001).

In natural regeneration systems it is assumed that regeneration will occur naturally (Grieser Johns 1997), beginning with an acceptable production of seedlings – some of which eventually become harvestable adult trees. The guidelines to ensure natural regeneration are usually designed to conserve the soil and seedling pool and to spare seed sources and pole-sized juveniles of the desirable species (Bruenig 1993). Rarely, however, do these prescriptions explicitly consider conservation of the basic ecological processes involved in natural regeneration – such as pollination, seed dispersal, seed predation, and seedling establishment. Since animals play important roles in these processes, it is conceivable that impacts of logging on the native fauna can directly and indirectly influence natural regeneration and long-term commercial productivity.

A vast number of studies have investigated the role that seed dispersal plays in the regeneration of tropical trees in natural forests (Gilbert 1980; Howe 1984; Terborgh 1986a, b, 1990; Bawa and Krugman 1991; Janzen and Vázquez-Yanes 1991; Chambers and MacMahon 1994; Hartshorn 1995; Ter Steege *et al.* 1996). Seed dispersal promotes offspring survival by linking seed sources to suitable establishment sites, making this process a priority for consideration when designing forest management systems. Sustained production of timber requires adequate recruitment of timber species seedlings from continuous seed input. Appropriate seed sources, however, are scarcer in logged forests because many reproductive individuals have been harvested. Management must plan carefully, therefore, to protect not only an adequate number and distribution of seed trees, but also the dispersal agents critical to moving seeds to suitable establishment sites.

This chapter deals with the possible consequences of selective logging and silvicultural procedures on seed dispersal by vertebrates. Studies that examine how logging actually influences vertebrate-mediated dispersal do not exist, but there is abundant literature on how logging affects fauna, on processes of seed dispersal and seedling establishment, and on natural regeneration. We searched for patterns in this literature, but the statements we make often lack direct empirical support. After a brief introduction to the field of seed dispersal, we will address four questions:

- How important are vertebrates for seed dispersal of tropical timber species?
- How might selective logging influence vertebrate seed disperser fauna?
- How can changes in vertebrate disperser fauna influence seed dispersal?
- What may be the ultimate consequences of logging-disperser interactions for the regeneration of timber species?

We conclude with some recommendations for forest management and research.

2.2 The importance of seed dispersal

Seed dispersal – the transport of seeds away from a parent plant – is an important process in the regeneration of most higher plants. Its evolutionary importance is illustrated by the mechanisms and structures of plants that promote seed dispersal. Dispersal modes can often be recognized by morphological characteristics of fruits and seeds, such as wings or panicles for wind dispersal, release mechanisms for explosive dispersal, sweet or nutritive fruit pulp for dispersal by frugivorous animals, nutritive nuts for dispersal by granivorous animals, adhesive structures for dispersal in furs, and airy tissues for dispersal by water (Van der Pijl 1982). Plant species often have more than one dispersal mode.

Seed dispersal is advantageous to plants when it enhances seed survival and increases reproductive success, and it may do so in various ways. First, dispersal reduces the risk of distance- or density-dependent mortality. Janzen (1970) and Connell (1971) introduced the idea that tropical forest tree seed survival increases with distance from the parent plant, because their seeds and seedlings suffer disproportional mortality due to predation and disease where they occur in high concentrations. The presence of stem canker in juveniles of the bird-dispersed canopy tree *Ocotea whitei* (Lauraceae), for example, is more likely to occur close to conspecific adult trees (Gilbert *et al.* 1994).

Hammond and Brown (1998) reviewed experiments that test whether seed predation conforms to the Janzen-Connell model, and concluded that invertebrate attack generally did, while vertebrate attack generally did not. In a study by Fragoso (1997), bruchid beetle larvae killed 77% of *Maximiliana* palm seeds remaining near parent trees, but less than 1% of seeds dispersed away from parent trees by tapirs (*Tapirus terrestris*). Species that suffer heavy seed predation by insects are very common in tropical forests, and include timber species such as *Peltogyne* spp., *Hymenea courbaril* (both Caesalpiniaceae) and *Aspidosperma* spp. (Apocynaceae) in Guyana (Ter Steege *et al.* 1996), *Virola nobilis* (Myristicaceae) in Panama (Howe *et al.* 1985), and *Mimusops bagshawei* (Sapotaceae) in Uganda (Chapman and Chapman 1995). Seed dispersal appears to be an essential survival mechanism for tree species that are heavily attacked by invertebrate seed predators.

Photo 2.1 Spiny rats (*Proechimys* spp.) can be seed dispersers rather than only seed predators.

Second, seed dispersal theoretically enhances a plant's chance to place seeds in suitable establishment sites (Hamilton and May 1977). Any increase in the average distance over which seeds are transported in random directions results in an exponential increase of the area over which seeds are distributed, with a larger area likely to include more suitable establishment sites. Dispersal can also be directional towards suitable sites, for instance, by *Rhinodemmys* tortoises that move between gap areas (Moll and Jansen 1995). At least some distance-related gain in seed and seedling survival may be attributed to a higher probability of encountering high light environments where invertebrate attack is likely less severe and seedling vigor is greater (Hammond and Brown 1998; Hammond *et al.* 1999).

Third, dispersal may improve germination when it involves passage through the gut of animals (Traveset 1998). The activity of chimpanzees (*Pan troglodytes*) (Wrangham *et al.* 1994) and forest elephants (*Loxodonta africana*) (Chapman *et al.* 1992) has suggested such enhancement. In some cases, gut passage may even be obligate. Seeds from *Calvia major* (Sapotaceae), for instance, require passage through the gut of large birds (Temple 1977; Janzen 1983). Other plant species require handling by animals to release seeds from the fruits, or to get seeds into suitable condition for germination. Seeds of *Chrysophyllum lucentifolium* (Sapotaceae), for example, suffer heavy predation by frugivorous insect larvae when they are not removed from fruit pulp (P.A. Jansen, personal observation), while *Bertholletia excelsa* (Lecythidaceae) needs agoutis to gnaw open the extremely hard fruit (Peres *et al.* 1997). Other species need to be buried by scatterhoarding rodents (Leigh *et al.* 1993), such as the Guianan timber species *Vouacapoua americana* (Caesalpiniaceae; Forget 1990). Burial by rodents may also be accompanied with the inoculation of mycorrhizae (Janos *et al.* 1995).

Other possible advantages of seed dispersal are colonization, area extension, and gene flow. Even if plants are able to regenerate in the same locality time and again, taxa that move or extend their populations may do better because they avoid inbreeding and are better able to track long-term climatic changes. The avoidance of interactions with siblings is also of possible importance (e.g., Willson 1992). For general reviews of seed dispersal and the advantages it brings to plants, see Ridley (1930), Van der Pijl (1982), Howe and Smallwood (1982), Willson (1992), and Venable and Brown (1993). Reviews specific to animal-mediated seed dispersal include McKey (1975), Janzen (1983), Howe (1986), Jordano (1992), and Stiles (1992).

The evolutionary importance of seed dispersal remains poorly understood because the fitness consequences of seed dispersal have rarely been measured. Indirect evidence, however, argues for the importance of seed dispersal. One can conclude that dispersal enhances the chances of seed survival, as well as the probability of suitable site colonization. Both aspects are of interest to forest managers where timber species are concerned.

2.3 Vertebrates as dispersers of tropical trees

The high species and generic richness of frugivorous (species with more than 50% of their diet composed of fleshy fruits) birds, bats and primates in the three tropical regions (e.g., Snow 1981; Fleming *et al.* 1987) illustrates the importance of vertebrates as seed dispersers in tropical forests. Neotropical examples of seed-dispersing frugivores are toucans (Howe 1977; Howe and Vande Kerckhove 1981), guans (Howe and Vande Kerckhove 1981), cotingas (Snow 1982), fruit bats (Fleming and Heithaus 1981; Fleming 1986), howler monkeys (Estrada and Coates-Estrada 1984, Julliot 1996) and spider monkeys (Van Roosmalen 1985). African examples include hornbills (Whitney *et al.* 1998), bulbuls (Graham *et al.* 1995), tauracos (Gautier-Hion *et al.* 1985; Sun *et al.* 1997), gorillas (Tutin *et al.* 1991), chimpanzees (Wrangham *et al.* 1994), baboons (Lieberman et al. 1979), and cercopithecine monkeys (Gautier-Hion *et al.* 1985). Australian-Asian examples include hornbills (Grieser Johns 1997), fruit pigeons (Crome 1975; Snow 1981), birds of paradise (Beehler 1983), cassowaries (Stocker and Irvine 1983; Willson *et al.* 1989), flying foxes (Fujita and Tuttle 1991; Richards 1995), gibbons (Whitington and Tresucon 1991), and macaques (Balasubramanian and Bole 1993).

Tropical dispersers are also found among other vertebrate groups. Ungulates implicated in seed dispersal include African duikers (Gautier-Hion *et al.* 1985; Feer 1995) and elephants (Alexandre 1978; Chapman *et al.* 1992; White *et al.* 1993; Parren and De Graaf 1995; Yumoto *et al.* 1995), Neotropical tapirs (Fragroso 1997), Asian rhinoceros (Dinerstein and Wemmer 1988), and deer (Balasubramanian and Bole 1993). Examples of seed-dispersing reptiles include tortoises (Rick and Bowman 1961; Moll and Jansen 1995), while seed-dispersing rodents include spiny rats (PHOTO 2.1; Gautier-Hion *et al.* 1985; Hoch and Adler 1997) and agoutis (Forget 1990; Hallwachs 1993). Even tropical fish can disperse seeds (e.g., Gottsberger 1978; Horn 1997).

A large percentage of tropical forest plant species produce fleshy fruits or arillate seeds, which are associated with seed dispersal by animals (TABLE 2.1; Howe and Smallwood 1982; Willson *et al.* 1989). Approximately 70% of woody plants in wet forests – and 35 to 70% in dry forests – produce such seeds (Gentry 1982; Willson *et al.* 1989). In the Neotropics, species with fleshy fruits may account for up to 90% of all woody plant

Table 2.1 Proportions of tree species with fleshy fruits in different tropical forests of the world (based on Howe and Smallwood 1982 and Willson *et al.* 1989)

Location	Forest type	No. of species considered	Percentage fleshy-fruited	Source
America				
Ecuador (Rio Palenque)	Wet	241	92	Gentry 1982
Costa Rica (La Selva)	Wet	161	91	Frankie *et al.* 1974
Colombia (Alto Yunda)	Wet	133	89	Hilty 1980
Costa Rica (La Selva)	Wet	320	65	Hartshorn 1978
Panama (BCI)	Moist	422	81	Gentry 1982
Costa Rica (Santa Rosa)	Dry	198	68	Gentry 1982
Costa Rica (Guanacaste)	Dry	104	51	Frankie *et al.* 1974
Africa				
Gabon (Makakou)	Wet	136	71	Hladik & Miquel 1990
Cameroon (Dja)	Moist	372	83	Sonke 1998
Ghana (Kade)	Moist	115	60-78	Hall & Swaine 1981
Nigeria (Okomu)	Dry	180	46-80	Jones 1955, 1956 *
Asia				
Borneo (Mount Kinabalu)	Wet	360[a]	35-40	Stapf 1894 *
Malaysia	Wet	?	>67	Raemakers *et al.* 1980 in Willson *et al.* 1989
Australia				
Australia (Queensland)	Wet	774	84	Willson *et al.* 1989
Australia (Queensland)	Wet	?	76-100	Willson *et al.* 1989
Australia (Queensland)	Dry	?	18-63	Willson *et al.* 1989

[a] Includes other plant species, not just trees

* In Howe and Smallwood 1982

species (Howe and Smallwood 1982). Vertebrates might even disperse species whose fruits are not fleshy, as many nut-bearing plant species are dispersed by granivorous birds and mammals.

Scientific information on the reproductive biology of tropical timber species is generally scarce (Hartshorn 1995; Hammond *et al.* 1996), and little is known about the importance of seed dispersal by animals for most of these species. Vertebrate-mediated dispersal is probably as common among timber species as among tree species in general. In the Guianas, for example, 72% of all 95 timber species are primarily vertebrate-dispersed (Hammond *et al.* 1996), while 74% of all 46 timber species in Bolivia appear to be animal dispersed (P.A. Zuidema, unpublished data).

Yet, vertebrate-mediated dispersal is not predominant among the tropical timber tree species that currently dominate the world market (TABLE 2.2; Putz *et al.* 2001). Roundwood volumes of species primarily dispersed by vertebrates account for only 18, 33 and 47% of the production from Australia-Asia, America and Africa, respectively. This is due to the fact that the timber market (and consequently forest exploitation) is still focusing on a very limited subset of all potential timber species (Grieser Johns 2001). In Peninsular Malaysia, for example, 16% of the 2,500 tree species have commercial potential, but only 1% plays a significant role at the international market (Grieser Johns 1997). The marketed subset over-represents long-boled emergent species, which are typically wind-dispersed. Proportions of animal-dispersed species are expected to increase as the market for lesser-known timber species increases. One example of an area where this diversification has begun is Fazenda 2 Mil in Brazil, where the CELOS silvicultural system is practiced and 74% of 46 exploited species are vertebrate-dispersed (De Camino 1998; N.R. De Graaf, personal communication).

Asia has lower proportions of vertebrate-dispersed timber species than Africa and the Neotropics. This is because a large proportion of Asian timber species are Dipterocarpaceae, which are generally known as (poorly) wind-dispersed or self-dispersed (Ashton 1988). Dipterocarp seeds, however, are often nutritious and commonly harvested by rodents that store them in spatially-scattered caches (Ashton 1988). Such cached seeds may be in better environments for germinating and developing than unharvested seeds (Jansen and Forget 2002). Dispersal of winged pine seeds by seed-hoarding *Tamias* squirrels in Nevada has been shown to be superior to wind dispersal (Vander Wall 1994), even though the trees appear morphologically adapted for the latter. Aspects of the fruiting strategy of Dipterocarps (large, nutritious seeds, mast fruiting) conform well to rodent dispersal (cf. Vander Wall 1990). Although rodents do not carry Dipterocarp seeds very far, and will consume part of their food reserves later, these seedeaters may have a positive net effect on the survival of Dipterocarp seeds. Animals may thus be important agents for secondary seed dispersal in Asian timber species.

2.4 Effects of Logging on the Disperser Fauna

Logging operations and silvicultural treatments induce changes in the vertebrate fauna of a forest, both directly and indirectly. Populations of some species decline, while others become more common. Changes in the population of frugivorous and granivorous birds and mammals can be brought about by physical alterations to the habitat, alterations of food availability, and increased hunting pressure. How each of these mechanisms affect seed disperser fauna is not clear because it is difficult to distinguish the effects of physical alterations from those altering food availability. Studies examining these processes are also not always comparable because they differ in methodologies, length of evaluation periods, and degree of control for edge effects and indirect effects such as hunting.

Physical alterations to the habitat

Physical alterations to the habitat due to logging and silvicultural measures often deviate from natural levels of disturbance (Chapman and Fimbel 2001). For example, logging creates new gaps that are usually larger than natural ones (Struhsaker 1997; Putz *et al.* 2001). As a result, gap environments increase from 1% to 10-20% at low extraction levels (Crome *et al.* 1992; Johns 1992a; White 1994b), to almost 50% at higher levels (Uhl and Vieira 1989). Logging usually kills many more trees than those extracted (Grieser Johns 1997). Johns (1988), for example, found that harvesting as few as 3.3% of the trees of dbh >9.5cm in a Malaysian forest resulted in an overall loss of more than 50% of individuals in this category. Other physical effects of logging are habitat destruction and fragmentation through access roads (Ter Steege *et al.* 1996) and clearings. Consequently, interior forest environments may become scarce in logged forests (Struhsaker 1997).

Frugivorous and granivorous animals are sensitive to these habitat alterations (Janzen and Vázquez-Yanes 1991), but vary in the way they respond. Moderate disturbance can favor certain dispersers, while negatively impacting others (Janzen and Vázquez-Yanes 1991). Bird diversity strongly declined with logging in French Guyana (Thiollay 1992), and significant declines in primate populations have been found several years after logging in many forests (Skorupa 1988, cited in Grieser Johns 1997; Struhsaker 1997). Animals that benefit from the denser undergrowth following habitat disturbance include the tapir in Brazil (Fragoso 1990), duikers in Sierra Leone (G. Davies cited in Grieser Johns 1997), forest elephants in Uganda (Struhsaker 1997), opportunistic frugivorous birds in Indonesia (Lambert 1992; Danielsen and Heegaard 1995), and rodents (Struhsaker 1997). Some species, such as the red-rumped agouti (*Dasyprocta agouti*), seem unaffected (Ter Steege *et al.* 1996).

Alteration of the availability of food

Logging and silvicultural treatments can also alter the availability of food. Logging may not necessarily affect the overall *quantity* of food. Plants remaining after logging may use the greater resource availability in logged-over forest to increase their production of leaves, flowers and fruits (Johns 1988; cf. Levey 1988a, 1990; Janzen and Vázquez-Yanes 1991). This increased production can buffer the loss of food plants due to logging, although the overall amount of fleshy fruit still tends to be lower in logged forests (Johns 1991b; Grieser Johns 1997). Many frugivorous mammals and birds are able to partially shift their diets towards folivory or insectivory or adapt their foraging behavior. Obligate frugivores such as spider monkeys, diana monkeys (*Cercopithecus diana*) and fruit bats, however, may be scarcer in logged-over forest (Grieser Johns 1997).

Logging and silvicultural operations, however, are likely to affect the *quality* of food resources, particularly when certain species of trees and climbers are selectively removed. Logging can result in a severe decline or even elimination of reproductive individuals of particular timber species (Lambert 1991; Grieser Johns 1997), especially those that are rare or that start fruiting above the minimum diameter for logging (Plumptre 1995). The impact of this on the frugivore fauna might be severe, as many species depend on a very limited set of food plant species during periods of low fruit availability. Such periods occur in most tropical forests (Hilty 1980; Howe and Smallwood 1982; Leighton and Leighton 1983; Gautier-Hion *et al.* 1985; Sabatier 1985; Heideman 1989; Van Schaik *et al.* 1993; White 1994a).

Some timber species may even be 'keystone' food resources that determine frugivore population levels (Gilbert 1980; Terborgh and Winter 1980; Foster 1982; Leighton and Leighton 1983; Howe 1984; Terborgh 1986a; Lambert 1991; Peres 2000a). Harvesting and liberation thinnings might theoretically reduce the availability of keystone food resources to a level at which the disperser community is severely affected. No study, however, has convincingly demonstrated the existence of such a cascading effect. Some potential keystone food plants have been recognized among timber species. Examples are *Sterculia pruriens* (Sterculiaceae) and *Clathrotropis brachypetala* (Papilionaceae) in Guyana (Ter Steege *et al.* 1996), and various *Ficus* species in Bolivia (Fredericksen *et al.* 1999b).

BOX 2.1 A Neotropical seed disperser assemblage in the Sapotaceae tree family

Disperser assemblages of tree species may include an array of animal species, even when these tree species appear to be 'adapted' to seed dispersal by particular agents. For instance, the Guianan Sapotaceae family includes many species with a fruiting syndrome that appears to be monkey-directed – large, yellow to reddish fruits with sweet, juicy, odorous pulp and large seeds. In fact, spider monkeys (*Ateles paniscus paniscus*) and howler monkeys (*Alouatta seniculus*; PHOTO 2.2) are the main - if not only primary - dispersers of many species in this family (Van Roosmalen 1982; Julliot 1996).

Fruits and seeds that drop below the parent tree because the monkeys neglect or spoil them, however, are often eaten by an array of frugivorous and granivorous vertebrates that may act as effective secondary dispersers. While feeding on fruit pulp below parent trees of a smaller-seeded genus such as *Manilkara*, large frugivorous birds, such as trumpeters (*Psophia crepitans*), may also ingest and disperse seeds. In addition, many other animals are secondary dispersers for the Sapotaceae family, such as coatis (*Nasua nasua*), tayras (*Eira barbara*), tapirs (*Tapirus terrestris*), and reptiles such as tortoises (*Geochelone denticulata*) (P.A. Jansen, personal observation).

Secondary dispersal is also provided by agoutis (*Dasyprocta agouti*) and acouchis (*Myoprocta acouchi*), which harvest seeds larger than 1g (approximately) from the forest floor and bury them one by one in shallow, widely spaced caches (Forget 1990, 1993; Hallwachs 1993; P.A. Jansen, unpublished data). Most of these seeds are relocated and eaten (*i.e.*, killed), but those that escape predation may be in a very good position to establish.

Finally, most of the seeds that are ingested by monkeys pass the digestive tracts of these animals unharmed and are defecated in small clumps. An array of dung beetle species transport and bury these seeds while harvesting dung (Feer 1999). Tortoises ingest seeds while eating dung (P.A. Jansen, personal observation), and rodents harvest seeds from dung piles and bury them (Janzen 1982a; Hallwachs 1993; F. Feer and P.M. Forget, personal communication), providing (mostly short-distance) secondary dispersal.

Most potential keystone food plants, however, have no direct commercial value – such as the following trees: *Casearia corymbosa* (Flacourtiaceae) in Costa Rica (Howe 1977), *Musanga cecropioides* (Cecropiaceae) in Guinea (Yamakoshi 1998), and Myristicacaeae and Meliaceae in Borneo (Leighton and Leighton 1983). They also include palms in Peru (Terborgh 1986b), the Guyanas (Ter Steege *et al.* 1996), and Guinea (Yamakoshi 1998); figs in Costa Rica (Wheelwright *et al.* 1984), Peru (Terborgh 1986a), Malaysia (Lambert and Marshall 1991), Borneo (Leighton and Leighton 1983; Lambert and Marshall 1991; Harrison 2000), and Colombia (D. Rumiz, personal communication), but not in Africa (Gautier-Hion and Michaloud 1989); and lianas (e.g., Anonaceae in Asia; Leighton and Leighton 1983). Ironically, many of these keystone plants are categorized as 'undesirable species' in silvicultural systems, and are commonly suppressed. Figs in Borneo (and probably elsewhere), for example, are greatly affected by logging because they often grow on trees of commercial size and value (Leighton and Leighton 1983).

Increased hunting and live animal capture

Increased hunting and live animal capture, either for subsistence or commerce, are often a consequence of making forests accessible for logging operations. Regulation of hunting during and after logging is not commonly practiced. Hunting in tropical forests is well-studied (Redford 1992; Rumiz *et al.* 2001; Bennet and Gumal 2001; Wilkie *et al.* 2001), and harvest data (Ayres *et al.* 1990; Vickers 1990; Fa *et al.* 1995; Fitzgibbon *et al.* 1995; Peres 2000b) indicate that large mammals and birds (primates, ungulates, large rodents, large bats, hornbills, toucans, cracids) are commonly taken. These are the animals that account for most of the seed-disperser biomass, as well as the biomass of handled seeds. Large-bodied frugivores are particularly susceptible to hunting (Chapman and Chapman 1995; Plumptre and Grieser Johns 2001; Davies *et al.* 2001). Unregulated hunting may cause drastic declines in the population sizes – notably of primates and large mammals (Fragroso 1990; Glanz 1990; Mittermeier 1990; Ráez-Luna 1995) and large birds (Robinson *et al.* 1990; Silva and Strahl 1990) – and is therefore a severe threat to disperser fauna.

2.5 Consequences of logging for seed dispersal

Vertebrate-dispersed plants are more susceptible to dispersal failure than wind-dispersed plants (Willson 1992). This raises a question. How great is the risk that changes in the disperser fauna after logging will lead to reduced dispersal success or outright dispersal failure? Dispersal success, or 'effectiveness', is the product-sum of the quantity of seeds and the quality of dispersal. Dispersal quantity – the number of seeds that are dispersed – depends on the abundance of dispersers and the number of seeds each disperser takes. Dispersal quality reflects the probability that a given seed will produce a new adult, as a function of seed treatment and seed deposition. Low-quality dispersers kill seeds, or deposit seeds in unsuitable conditions, while high-quality dispersers enhance seed germination and/or deposit seeds in favorable environments (Schupp 1993).

Quantities of seeds dispersed

Quantities of seeds dispersed seem to be buffered against loss of dispersers by 'disperser redundancy' in most vertebrate-dispersed species. Tropical plants are typically dispersed by a variety of animal species that belong to different taxonomic groups (BOX 2.1). Their disperser assemblages are usually 'loose' and highly variable in space and time (Howe 1983; Jordano 1993, 1994; Fuentes 1995). Weak interactions between animals and plants are characteristic of species-rich tropical systems (Jordano 1987). It is likely, therefore, that reduced seed dispersal by one species can be compensated for by increased dispersal by other species (Janzen and Vázquez-Yanes 1991).

'Substitution' of one disperser species by another is possible and likely because dietary overlap between vertebrate dispersers is often great – even between different taxonomic groups (Janzen and Vázquez-Yanes 1991). On islands in the South Pacific, for instance, frugivorous pteropid bats are the most important dispersers of many plant species. In fact, these bats substitute for the large frugivorous birds that have been eliminated in recent historical time (Cox *et al.* 1991; Rainey *et al.* 1995). In the Neotropics, Janzen and Martin (1982) argue that certain plant species have persisted after the extinction of their original megafauna dispersers some 10,000 years ago, and Hallwachs

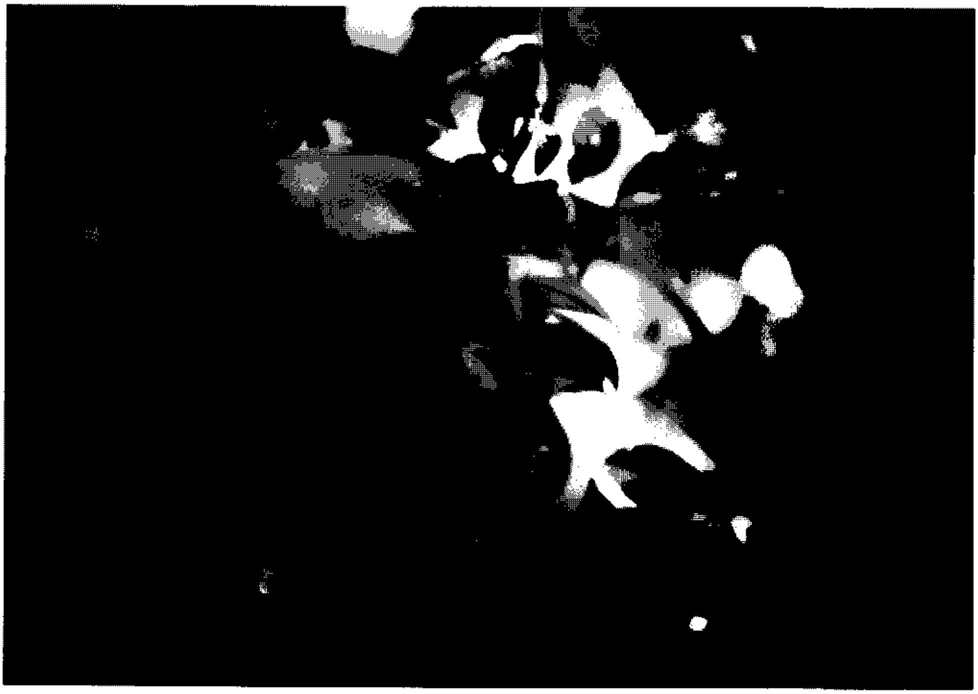

Photo 2.2 Red howler monkeys (*Alouatta seniculus*) are important dispersers for many plant species, including at least 86 tree species in the Nouragues rainforest reserve in French Guiana.

(1993) states that agoutis (*Dasyprocta punctata*) substitute for the long-extinct dispersers of the timber tree *Hymenaea courbaril*. Janzen and Vázquez-Yanes (1991) propose that free-ranging cattle and horses also substitute for the original ungulate dispersers of the Central American tree *Crescentia alata* (Bignonaceae).

Plants having one or very few disperser species are at risk of dispersal failure, and certain animals might be keystone dispersers for these plants (Futuyma 1973; Howe 1977; Gilbert 1980). Species with few dispersers, however, appear to be uncommon. Well-known examples include the timber species *Cola lizae* (Sterculiaceae) in Gabon, where the only known disperser is the lowland gorilla (*Gorilla gorilla gorilla*; Tutin *et al.* 1991), and *Hymenaea courbaril* (Caesalpiniaceae) in Costa Rica that is principally dispersed by agoutis (Hallwachs 1993; Asquith *et al.* 1999). Bond (1995), in his investigation of plant extinction due to pollinator or disperser failure, found no clear case of plant extinction as a result of the loss of its dispersers. One possible example, however, is the regeneration failure of the tree *Calvaria major* as a result of the absence of obligatory seed processing by its historical disperser, the dodo (*Raphus cucullatus*; Temple 1977).

While there is redundancy in vertebrate-mediated dispersal in most plants, this does not imply that dispersal processes are not sensitive to logging. Large-seeded tree species may depend on disperser species that are particularly susceptible to logging and associated hunting practices. Moreover, the loss of any given disperser species may affect a range of plant species. Hornbills, for example, disperse *Guarea* sp., *Celtis mildbraedii*, *Maesopsis eminii*, *Canarium schweinfurtii* and at least 30 other tree species that are exploited for timber (Whitney *et al.* 1998). Red howler monkeys disperse at least 86 species of plants in forests of French Guiana (PHOTO 2.2; Julliot 1996). Many plant species on islands in the South Pacific risk losing their principal dispersers because flying foxes are an endangered group (Cox *et al.* 1991; Fujita and Tuttle 1991). The redundancy capacity of vertebrate-mediated dispersers in logged forests remains largely unknown, however, as no studies have compared relative quantities of seeds dispersed between logged and unlogged forests (but see Guarigata *et al.* 2000).

The quality of dispersal

The quality of dispersal may also be affected by changes in the disperser fauna because disperser species differ in the way they treat and deposit seeds (Levey 1986; Loiselle and Blake 1999). Passage through the digestive tract of one species might cue germination, while passage in another species might kill the majority of seeds (Traveset 1998). One disperser might carry seeds further and deposit seeds in more favorable conditions than another (Schupp 1993). Of the many animals that forage in fruiting trees, very few may actually be good dispersers (Howe 1977).

Any change in the disperser assemblage is likely to influence dispersal quality, even if the total quantity of seeds dispersed remains constant (Janzen and Vázquez-Yanes 1991). Many species that are vulnerable to logging are considered high-quality dispersers, even though their dispersal qualities have not actually been measured. This is particularly true for large animals, as they are capable of transporting seeds further than most small animals. Lower dispersal quality leads to fewer seeds surviving disperser handling, fewer seeds leaving the vicinity of the parent tree, and more seeds being deposited in clumps rather than being scattered (Howe 1989).

We can conclude that changes of the vertebrate disperser fauna due to logging may be at the cost of both quantity and quality of seed dispersal. The risk of poor dispersal holds particularly true for species commonly dispersed by highly frugivorous vertebrates and large mammals. Such species commonly are relatively large-seeded. In the following section, we attempt to evaluate the consequences of poorer dispersal for the natural regeneration of these 'risk-species'.

2.6 Possible consequences of poor dispersal for natural regeneration

Several researchers have claimed that it is critical for the preservation of natural tropical forests to maintain the animals that facilitate seed dispersal (e.g., Howe 1984; Pannell 1989; Chapman *et al.* 1992). Poor dispersal should lead to decreased seedling recruitment because fewer seeds reach suitable sites. Those that do still may suffer distance- and density-dependent mortality. This would threaten the long-term persistence of tree species that are unable to recruit under conspecific adults (Chapman and Chapman 1995). While logging can reduce the quantity and quality of seed dispersal (see above), changes in microenvironment after logging may offset lower dispersal rates through enhanced germination and survivability of seeds (Oliver and Larson 1990). This raises the question of whether enhanced seed and seedling survival in logged-over forests counterbalances poor dispersal of risk species?

Logged-over forest often has higher individual seed and early seedling survival because more gap environments are available. Risk species tend to be large-seeded and shade-tolerant, and these do well in gap edges and small gaps (but not in the core area of large gaps) (Kasenene and Murphy 1991; Hammond and Brown 1995; Zagt and Werger

Photo 2.3 Roads constructed for timber extraction also provide access for commercial hunting, affecting especially the important vertebrate seed dispersers.

1998). Their poor performance in gap centers may be linked to their vulnerability to high temperatures and water stress (Whitmore 1991; Brown and Whitmore 1992; Hammond and Brown 1998). Reduced dispersal in logged forests may be counterbalanced if low impact logging measures are applied (Mason and Putz 2001; Laurance 2001) – as minimum disturbance to forest structure helps to create small gap sizes that are of benefit to many risk species (Veenendaal *et al.* 1996; Van der Meer *et al.* 1998). Seed and seedling mortality due to biotic sources may also be lower in logged-over forest. The drier conditions under increased canopy openness tend to reduce fungal attack on seedlings. Greater light availability also enhances the growth of seedlings, making them less susceptible to diseases and predation than seedlings in understory conditions (Hammond and Brown 1998; Hammond *et al.* 1999).

How logging affects levels of post-dispersal seed predation is not well known (Janzen and Vázquez-Yanes 1991). Rodents tend to become more common in logged-over forest, and the dense vegetation may also attract browsers (e.g., deer and elephants) that hamper recruitment (Struhsaker 1996). Asquith *et al.* (1997) found that the removal of larger mammals resulted in increased seed predation and seedling hervibory by rats on small islands.

Notwithstanding, it is not clear what the net effect of logging is on seedling recruitment (Guarigata and Pinard 1998). So far, there is no conclusive evidence of the long-term sustainability of existing tropical natural regeneration systems (Whitmore 1990; Grieser Johns 1997; N.R. de Graaf, personal communication). Not only may forest growth be over-estimated (Bossel and Krieger 1991; Grieser Johns 1997), but it is also uncertain whether natural regeneration and the recruitment of timber species is sufficient (Frederickson and Mostacedo 2000). Stimulating the survival and growth of 'potential crop trees' does not always increase short-term timber production (De Graaf *et al.* 1999), nor does it contribute to the population growth required for long-term production. While seedling recruitment seems to be the bottleneck, little is known about the reproductive ecology and establishment requirements of most timber species (Bongers 1998).

Whichever way one looks at it, logging appears to give timber species a comparative disadvantage due to the harvesting of seed sources (and the vulnerability of some of their dispersal systems), which may result in low rates of seedling recruitment relative to nontimber species (Bongers 1998). These disadvantages can be mitigated by offering juveniles a selective advantage through silvicultural measures (refinement and liberation), but these measures are expensive and might negatively affect food availability for the disperser community.

Given our current knowledge, guidelines to ensure recruitment are limited. Sparing the reproductive individuals of timber trees and protecting soils are essential requirements for providing available seed material and establishment sites, but do not guarantee recruitment. Trees may produce increased seed yields through higher availability of resources (light, nutrients) and less intense predispersal seed predation – but only if they survive habitat alteration due to logging and if there is sufficient pollination (Janzen and Vázquez-Yanes 1991). Seeds of timber species, therefore, should be viewed as an invaluable resource. Any measures that promote seed dispersal may contribute to a better use of this resource by enhancing net seed survival, and will be in management's interest.

2.7 Conserving seed dispersal processes in logged forest

Management options

The availability of vertebrate dispersers in a logged-over forest depends on the availability of critical food resources, suitability of the habitat, and the hunting pressure. Forest management guidelines to foster seed dispersers should therefore be aimed at ensuring the year-round availability of the food resources required by dispersers, minimizing habitat alteration, and restricting the hunting of known dispersers. These approaches are being tested and evaluated at a number of sites in the tropics (Grieser Johns 2001; Fimbel *et al.* 2001; Donovan 2001) – including Fazenda 2 Mil, Manaus Brazil, where an extended form of the CELOS silvicultural system is being applied (De Graaf 1986; De Camino 1998).

Protecting food availability

Protecting the most important food plants – especially potential keystone food plants – during all silvicultural operations can probably ensure food availability most effectively for seed dispersers. One way to minimize the reduction of overall food availability to dispersers is reduced-impact logging (Mason and Putz 2001; Laurance 2001). At Fazenda 2 Mil in Brazil, a 100% inventory of harvestable trees (and some other woody plants) precedes every harvesting operation. The function of trees and other woody plants as food resources (and seed sources) are taken into account when planning harvesting, liberation, or refinement. Students conducted a literature and field survey to identify which food plants are locally important for monkeys (N.R. De Graaf, personal communication). The goal of these efforts is to use careful planning to avoid endangering the food supply of seed dispersers.

Minimizing habitat alteration

Habitat alteration due to logging is unavoidable. It can, however, be limited by reduced-impact logging procedures (Hendrison 1990; Mason and Putz 2001; Laurance 2001). Setting aside reserve areas can further mitigate the effects on fauna and corridors that are left undisturbed (Marcot *et al.* 2001). Specific requirements of particular dispersers, if known, can also be incorporated into management planning. At Fazenda 2 Mil, careful planning and preparation of felling (including vine cutting and directional felling) and skidding are standard procedures designed to minimize damage and habitat alteration. The concession area also includes 10% of its area in reserves (N.R. De Graaf, personal communication).

Controlling hunting

Hunting seed dispersers should be avoided or at least not exceed the sustainable harvest (e.g., Robinson and Redford 1991). To achieve this, effective regulation is indispensable. At the Fazenda 2 Mil concession, hunting and gathering animals that disperse seeds is strictly forbidden. Employees (many of whom are hunters) are informed about the reasons, and the company sees to it that alternatives for wild meat are available (N.R. De Graaf, personal communication).

Applying these criteria requires a basic knowledge about the reproductive ecology of timber tree species, including an understanding of which vertebrates are important seed dispersers. Habitat and food requirements (or at least which plants are their most important food resources) of these animals must also be known. For most forest areas, such information still needs to be collected. Because the same plant species may have different dispersers in different forests, and the same animals may have different sets of important food species, it would be safest to have such information at the management (or concession) level.

Research priorities

Very little is known about how silvicultural procedures influence seed dispersal and seedling recruitment. Understanding where and how logging influences disperser fauna – and at what point natural regeneration might be jeopardized due to negative environmental impacts on these animals – is basically a 'trial and error' matter (Janzen and Vázquez-Yanes 1991). To address this paucity of information it is recommended that research focus on several areas. First, there is a need for research that actually measures the fitness consequences of seed dispersal. Such a study could, for instance, compare the fates of entire cohorts of seeds in areas with and without disperser(s).

Second, there is a clear need for field studies of how silvicultural procedures affect habitat suitability and year-round availability of food for seed dispersers. The identification of keystone food plants for dispersers would be indispensable. This information is testable by comparing frugivore population levels between large forest patches (from which only keystone foods are experimentally removed), untreated forest patches, and forest patches with random experimental removal of food plants up to a comparable level of reduction (Fimbel *et al.* 2001).

Third, we need to know how changes in disperser fauna influence the effectiveness of seed dispersal. Seed/seedling distribution patterns, and seed/seedling survival rates between forest patches with and without (or with fewer) individual dispersers could be compared. Comparable locations with different levels of hunting might be suitable sites for such studies. Quantifying dispersal effectiveness of different species, determining what proportions and absolute quantities of seed removed by different species are influenced by the relative abundance of these species, and evaluating the effects of changes in disperser fauna on dispersal effectiveness by modeling are other approaches needing evaluation. With such studies, we could also try to answer the questions raised by Schupp (1993): Are there dispersers that maximize both the quantity and quality of dispersal? Is quantity or quality more important for effective dispersal? How variable is the dispersal quality of a disperser for different plant species?

Fourth, we still need to know much more about how silvicultural procedures influence the availability of recruitment sites – especially for timber species. We must first collect basic information on the reproductive ecology and establishment requirements of these species and others of commercial, ecological, and social importance. More theoretical and empirical studies are also needed on how the environment influences plant survival and growth in order to determine what levels of seedling stocking are required for reaching the sustained yields of timber that are commonly envisioned.

2.8 Acknowledgments

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Table 2.2 Role of vertebrates in seed dispersal of the most important timber species for three tropical regions in terms of volumes exported by ITTO-member countries during 1994-1996.

Species	Volume (10^3 m^3) [a]	Role of animals [b]
America		
Cedrela spp. (Meliaceae)	1,767.1	-
Swietenia spp. (Meliaceae)	1,217.5	S
Hymenaea *courbaril (Leguminosae)*	926.3	P
Tabebuia spp. (Bignonaceae)	502.9	-
Araucaria angustifolia (Araucariaceae)	240.0	P
Dinizia excelsa (Leguminosae)	171.4	S
Catostemma commune (Bombacaceae)	164.0	P
Ocotea spp. (Lauraceae)	119.8	P
Virola spp. (Myristicaeae)	107.7	P
Bagassa guianensis (Moraceae)	82.9	P
Brosimum *utile (Moraceae)*	75.7	P
Carapa guianensis (Meliaceae)	71.7	P
Ochroma lagopus (Bombacaceae)	64.0	S
Amburana spp. (Leguminosae)	58.3	S
Trattinickia spp. (Burseraceae)	28.0	P
Peltogyne pubescens (Leguminosae)	25.4	P
Platymiscium pinnatum (Leguminosae)	22.9	S
Vochysia spp. (Vochysiaceae)	16.0	-
Bowdichia nitida (*Leguminosae*)	11.4	-
Eperua falcata (Leguminosae)	6.9	P
Mora excelsa (Leguminosae)	6.4	S
Cordia goeldiana (Boraginaceae)	5.7	P
Aspidosperma spp. (Apocynaceae)	3.4	-
Pouteria spp. (Sapotaceae)	2.9	P
Hyeronima spp. (Euphorbiaceae)	2.0	P
Goupia glabra (Goupiaceae)	0.3	P
Humiria balsamifera (Humiriaceae)	0.1	P
Other species	4,171.4	
Total	9,872.0	
Percentage of volume		
Primary dispersal by animals		33
Only (potential) secondary dispersal by animals		23
No dispersal by animals		42
Percentage of genera		
Primary dispersal by animals		59
Only (potential) secondary dispersal by animals		11
No dispersal by animals		26

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[a] Roundwood equivalents, calculated with 50% conversion efficiency for plywood and veneer, and 35% conversion efficiency for sawnwood.

Table 2.2 Continued

Species	Volume (10^3 m^3) [a]	Role of animals [b]
Africa		
Aucoumea klaineana (Burseraceae)	6,620.8	P
Guibourtia arnoldiana (Leguminosae)	3,087.2	S
Triplochiton spp. (Sterculiaceae)	2,936.8	-
Mitragyna ciliata (Rubiaceae)	2,167.2	-
Entandophragma spp. (Meliaceae)	2,050.8	-
Tieghemelia spp. (Sapotaceae)	1,314.3	P
Dacryodes spp. (Burseraceae)	1,255.0	P
Ceiba pentandra (Bombacaceae)	1,201.7	S
Chlorophora excelsa (Moraceae)	1,181.1	P
Khaya spp. (Meliaceae)	805.9	S
Baillonella toxisperma (Sapotaceae)	789.1	P
Terminalia spp. (Combretaceae)	759.1	S
Lophira alata (Ochnacaeae)	483.2	S
Antiaris africana (Moraceae)	435.8	P
Pycnanthus angolensis (Myristicaceae)	302.5	P
Aningeria spp. (Sapotaceae)	227.8	P
Erythropleum ivorense (Leguminosae)	153.0	P
Pterygota macrocarpa (Sterculiaceae)	131.8	S
Herietia utilis (Sterculiaceae)	111.8	S
Nauclea diderrichii (Rubiaceae)	97.5	P
Distemonanthus benthamianus (Leguminosae)	94.1	-
Piptadeniastrum africanum (Leguminosae)	87.8	S
Afzelia spp. (Leguminosae)	68.2	P
Gossweilerodendron balsamiferum (Legumosae)	60.6	S
Lovoa trichilioides (Meliaceae)	54.9	S
Pericopsis elata (Leguminosae)	49.7	S
Canarium schweinfurthii (Burseraceae)	49.5	P
Pterocarpus soyauxii (Leguminosae)	46.1	-
Distemonanthus spp. (Leguminosae)	42.0	-
Guarea cedrata (Meliaceae)	38.8	P
Other species	567.1	
Total	27,271.2	
Percentage of volume		
Primary dispersal by animals		47
Only (potential) secondary dispersal by animals		26
No dispersal by animals		27
Percentage of genera		
Primary dispersal by animals		43
Only (potential) secondary dispersal by animals		37
No dispersal by animals		20

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[b] Dispersal modes; - = no dispersal by vertebrates, P = primary dispersal by vertebrates, and S = only (potential) secondary dispersal by vertebrates.

Table 2.2 Continued

Species	Volume (10^3 m^3)[a]	Role of animals[b]
Asia		
Shorea spp. (Dipterocarpaceae)	14,559.5	S
Dipterocarpus spp. (Dipterocarpaceae)	4,531.1	S
Dryobalanops spp. (Dipterocarpaceae)	3,511.9	S
Anisoptera spp. (Dipterocarpaceae)	1,966.6	S
Homalium foetidum (Samydaceae)	863.0	-
Koompassia spp. (Leguminosae)	815.9	-
Tectona grandis (Verbenaceae)	698.0	P
Calophyllum spp. (Guttiferae)	674.0	-
Dactylocladus stenostachys (Crypteroniaceae)	594.8	P
Intsia spp. (Leguminosae)	573.4	P
Pouteria spp. (Sapotaceae)	504.0	P
Parashorea spp. (Dipterocarpaceae)	439.1	P
Copaifera palustris (Leguminosae)	388.6	P
Syzygium spp. (Myristicaceae)	358.4	P
Terminalia spp. (Combretaceae)	332.3	P
Celtis spp. (Ulmaceae)	310.9	P
Palaquium spp. (Sapotaceae)	302.4	P
Buchanania spp. (Anacardiaceae)	277.4	P
Canarium spp. (Burseraceae)	244.3	P
Calophyllum spp. (Guttiferae)	234.4	P
Gonystrylus bancanus (Thymelaeaceae)	231.3	P
Pterocymbium beccarii (Sterculiaceae)	213.9	-
Heritiera simplicifolia (Sterculiaceae)	208.9	S
Dillenia spp. (Dilleniaceae)	200.9	P
Pometia pinnata (Sapindaceae)	196.7	P
Hopea spp. (Dipterocarpaceae)	182.7	S
Xylia xylocarpa (Leguminosae)	179.5	?
Mastisciodendron spp. (Rubiaceae)	172.0	P
Agathis spp. (Araucariaceae)	171.4	S
Dyera costulata (Apocynaceae)	170.0	-
Other species	14,802.1	
Total	48,909.2	
Percentage of volume		
Primary dispersal by animals		18
Only (potential) secondary dispersal by animals		74
No dispersal by animals		8
Percentage of genera		
Primary dispersal by animals		57
Only (potential) secondary dispersal by animals		23
No dispersal by animals		17

Principal sources: Van Roosmalen 1985, and Hammond *et al.* 1996 for America; Hall and Swaine 1981, and Hawthorne 1985 for Africa; Soerianegara and Lemmens 1993, Lemmens *et al.* 1995, and Sosef *et al.* 1998 for Asia.

3. Scatterhoarding rodents and tree regeneration in French Guiana

3.1. 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 and Sabatier 1988), tortoises ingest seeds while feeding on dung of frugivorous mammals (B. Josseaume, personal communication), and dung beetles take and bury seeds with dung (Shephard and Chapman 1998; 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, a 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, rather than simply being detrimental.

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.

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 some directions for further research.

3.2 Patterns of seed removal and dispersal

Sabatier (1983) and Forget (1990) showed that the large seeds of the canopy tree *Vouacapoua americana* (Caesalpiniaceae), a 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) (personal observation). Rodents also appeared to remove a great variety of other seed species, among which large seeds of bird- and monkey-dispersed species, such as the Myristicaceae (Forget and Milleron 1991) and Sapotaceae (Forget *et al.* 2001), as well as large seeds of bat-dispersed species, such as the Lecythidaceae and Fabaceae (Forget 1992, 1993; personal observation).

Seed removal by acouchies and agoutis is also important in terms of numbers. Jansen and co-workers (unpublished data) 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% of cases of discovery, agoutis for less than 10%. Other important seedeaters, especially in terms of seed quantities removed at a time, were collared peccaris (*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.* 2001). 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 and Adler 1997; Adler and Kestell 1998) and larderhoard seed (Guillotin 1982), while the latter scatterhoard seed in trees (personal observation).

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%, 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 and 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 (e.g., FIGURE 3.1). In 1996, for instance, removal of *C. procera* seeds did not set off until production of the preferred species *Licania alba* had ceased completely (unpublished data). Then, the animals became interested in taking even old and germinated seeds of *C. procera*.

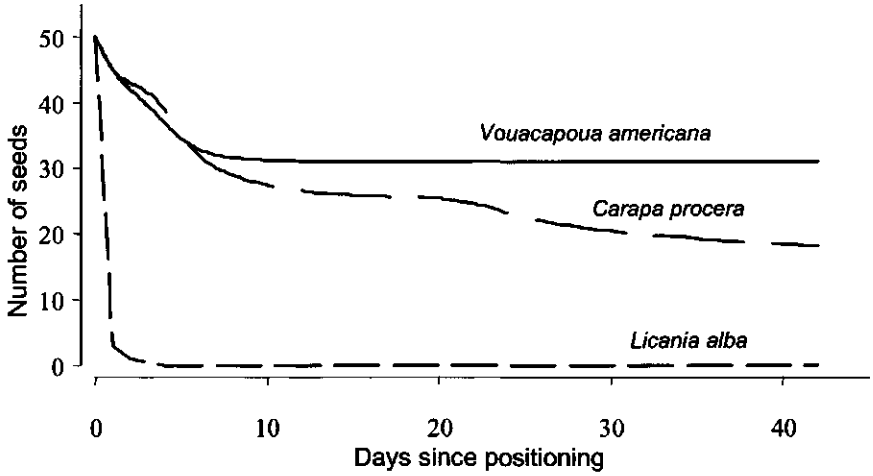

Figure 3.1 Removal of three scatterhoarded seed species. 50 seeds per species were placed at the forest floor along a transect with 2m inter-spacing, and 6m between conspecific seeds (n = 50). Nouragues, May 1996, P.A. Jansen and A. Siepel, unpublished data.

Forget (1990) laid out thread-marked *V. americana* seeds, and searched for them after their disappearance. He discovered that a great proportion (70%) was scatter-hoarded 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 125m (*Carapa* 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 (personal observation). FIGURE 3.2 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 50m search radius.

3.3 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 as 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.

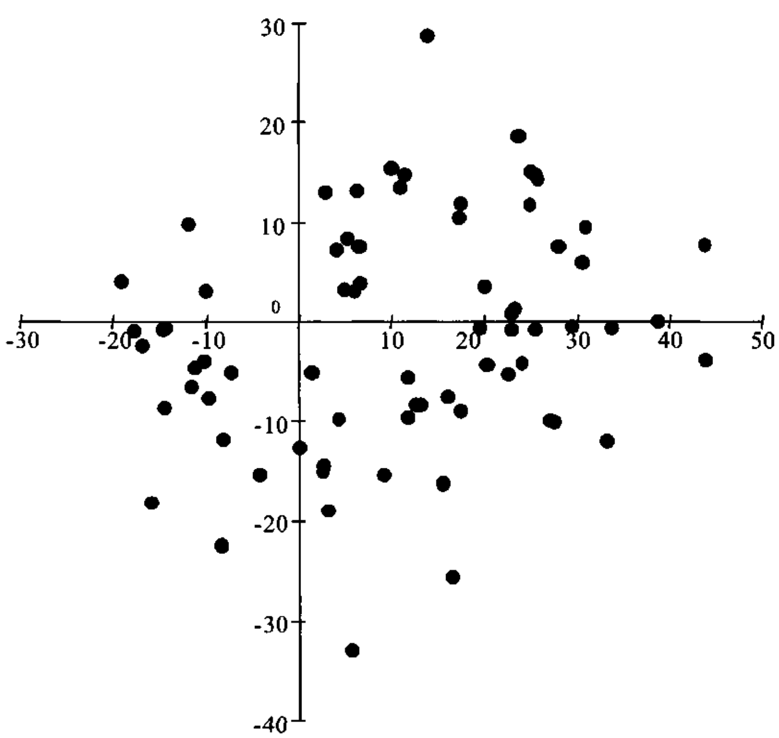

Figure 3.2 Spacing pattern of *Licania alba* seeds scatterhoarded by an acouchy. 52% of 139 thread-marked seeds taken from an artificial food source (origin) were relocated. Nouragues, May 1996, P.A. Jansen and A. Siepel, unpublished data.

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.

Selectivity and seed value

The amount of seeds 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

Table 3.1 Properties determining nutritional value and storage life of three 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 n = 25	*Carapa procera* n = 63	*Vouacapoua americana* n = 50
Nutritional value			
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 analyses were done in duplo on a mixture of three uninfected seeds.

example, prefer caching husked sunflower seeds to unhusked ones, since the former yield more net energy, as no investment in dehusking is required (Moreno and 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 and 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 (FIGURE 3.1), for instance, can be explained by differences in storage life and fat content (TABLE 3.1). 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).

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

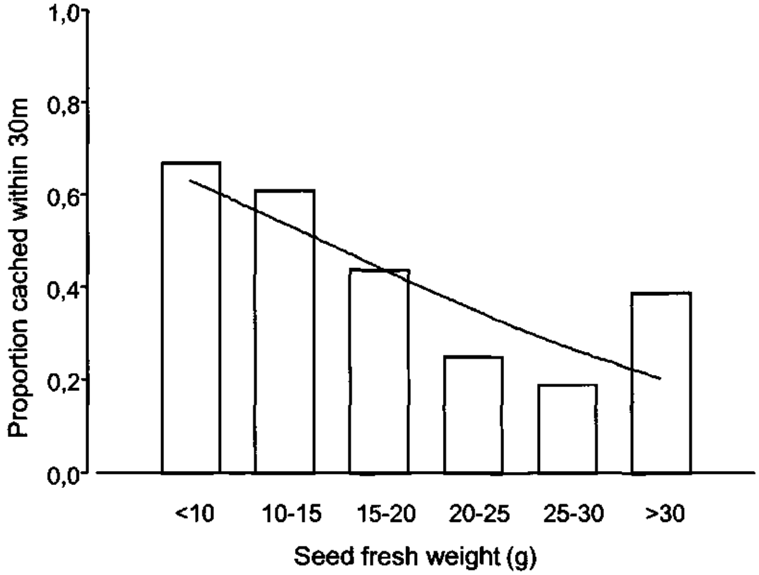

Figure 3.3 Proportion of *Carapa procera* seed cached within 30m from an artificial seed source by at least one acouchy. Larger seed were taken beyond 30m more often than smaller ones (*Logistic regression on binary data:* Wald=13.7, *p*<.0001). Nouragues, May 1995, P.A. Jansen, P.M. Forget and L. Van der Voort.

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 and 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 and Smith 1984; Waite and Reeve 1993; Jokinen and Suhonen 1995; Vander Wall 1995b; Forget *et al.* 1998; Leaver and 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 (FIGURE 3.3).

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, for example treefall gaps with tangles of lianas and tree crowns.

Cache properties

The fact that seed are often cached near or in objects, such as logs, and that seeds with hard endocarp are more common in soil near such objects than in the open (Kilty 1981) has 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 and Peterson 1996), squirrels (Jacobs and Liman 1991; MacDonald 1997), kangaroo rats (Jacobs 1992; Barkley and Jacobs 1998), and golden hamsters (Georgakopoulis and 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 6cm) than less valuable ones (e.g., *V. americana*, mostly hidden right below the surface) (unpublished data).

Cache management

Most cached seeds disappear within a few weeks after caching. Forget (1990) found that 57% 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 hide them. However, but 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 and 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 and 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 and Peters 1992) and jays (Waite and Reeve 1995) appear to behave in the same 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.

Photo 3.1 Red-rumped agouti (*Dasyprocta leporina*), manipulating a seed. Photo Tom Ruttink.

3.4 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 chapter discusses how scatterhoarding would increase the chances of seeds surviving, germinating and establishing if the rodents did not recover their caches.

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 and 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 and Brown 1998).

In temperate areas, experimentally scatterhoarded seeds indeed disappear more slowly at lower densities (Stapanian and Smith 1984; Clarckson *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; personal observation).

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 and 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 and 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 seed 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 and Bongers 1996). Alternatively, scatterhoarding could be advantageous simply because a regular spacing of seeds increases the number of independent chances of seeds hitting the patch-wise distributed canopy gaps.

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 and 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, after one month, *C. procera* seeds that had not been removed from experimental seed plots under adult trees in Paracou were all infested by moth (*n*=20 adult trees; 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 and 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; 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 and 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.

3.5 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 (*cf.* 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 chapter 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.

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 and 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 9.5m; Yasuda *et al.* 1991), but appeared to be unsuitable for tracking seed dispersed by acouchies (personal observation). The use of transmitters (Sone and 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 artifically 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 and 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 (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.

Photo 3.2 The canopy tree *Vouacapoua americana* (Caesalpinaceae) displays mast seeding: it produces a large crop of odorous nuts only once every few years.

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 naïve searcher for caches. While some scatterhoarders, such as Clarck's nutcracker (*Nucifraga columbiana*), remember caches for extremely long periods of time (Balda and Kamil 1992), diurnal rodents indeed tend to rather 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 unlogical, 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.

3.6 Evolutionary aspects

The interactions between scatterhoarding rodents and large-seeded trees have some interesting evolutionary aspects. If the net effect of scatterhoarding for plants is 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), coevolution of black walnut with fox squirrels (Stapanian and 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.

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 the 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 and 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 (SECTION 3.3). 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 boar, *i.e.* reduced seed predation below the parent plant. Rodents also tend to hide more valuable seeds more carefully than food of lower value (Stapanian and Smith 1986). Accordingly, larger seed tend to be transported further and spaced apart wider than smaller seeds (SECTION 3.3; Stapanian and Smith 1984; Forget *et al.* 1998), which might yield survival advantages (SECTION 3.4). 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 and 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.

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 (SECTION 3.4).

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 scarcity, 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.

Photo 3.3 Odorous nuts of *Licania alba* (Chrysobalanaceae) become available for dispersal only after the fruit has fallen to the forest floor and has dehisced by natural ripening.

3.7 Acknowledgements

The ideas presented in this paper have been formed by discussions with many different people, especially during various field trips. Although we are grateful to all of them, we would specifically like to thank Frans Bongers, Roel Brienen, Gérard Dubost, François Feer, Sander Koenraadt, Jan den Ouden, Anne Rutten, Almira Siepel, Leonie van der Voort, and Sip van Wieren for their contributions to discussions and field experiments. We thank Frans Bongers and Almira Siepel for their comments on the manuscript. The authors were supported by the Netherlands Foundation for the Advancement of Tropical Research with grant W84-407 (P.A. Jansen), by CNRS with Research support to UMR CNRS-MNHN 8571 and by the French Ministère de l'Environnement with programs SOFT 91208 and SOFT 95042 (P.M. Forget).

4. Rodents change perishable seeds into long-term food supplies

Seed-hoarding vertebrates are able to survive periods of food scarcity by creating long-term supplies during the preceding fruiting season. It is therefore paradoxical that these animals also stock up non-dormant seed species whose rapid germination depletes seed reserves before the rodents need them. We found that scatterhoarding acouchies in French Guianan rainforest actively managed their stock of *Carapa procera* seeds as to intervene in germination. By pruning the protruding germ, the rodents turned the seeds into 'living dead' suitable for long-term storage. Because scatterhoarding rodents and the *Carapa* seed type co-occur world-wide, the phenomenon of 'zombie seeds' is hypothesised to be widespread.

4.1 Introduction

Seasonal fluctuations in fruit availability can cause enormous stress for animals that depend on fruit and seed for food. Many granivorous vertebrates deal with these fluctuations by hoarding seeds during periods of fruit abundance, and draw upon these reserves during periods of scarcity (Vander Wall 1990). Seeds hoarded during fall, for example, are essential for winter survival of hoarding animals in temperate regions (Nilsson *et al.* 1993; Wauters *et al.* 1995), while seeds hoarded during the wet season determine whether tropical seed hoarders survive the dry season (Henry 1999). Because the time elapsing between caching seeds and actually needing them may be as long as several months, seed storage life is an important criterion for the choice of seed species for long-term supplies (Reichman 1988; Gendron and Reichman 1995; Hadj-Chikh *et al.* 1996). However, seed-hoarding mammals also store seed species with rapid germination, which transforms seed reserves into seedlings that have no food value for granivores. Why would animals store such seeds if they could not preserve them for use during the lean season?

We solved this riddle by studying how Red acouchies (*Myoprocta exilis*) manage their supply of *Carapa procera* (Meliaceae) seed in a French Guianan rainforest. Acouchies (FIGURE 4.2A) are common caviomorph rodents that 'scatterhoard' seeds by burying them in widely spaced, single-seeded soil or litter caches. Acouchies in French Guiana store abundantly available seeds in the wet season – February to June – to create supplies for the lean dry season – August to December. The peak of scatterhoarding – April to May (Forget *et al.* 2002) – coincides with peak seed production by *C. procera*, a common canopy tree species, whose large (~20g) fatty (~50% of endosperm dry weight) seeds are much sought after by granivorous mammals,

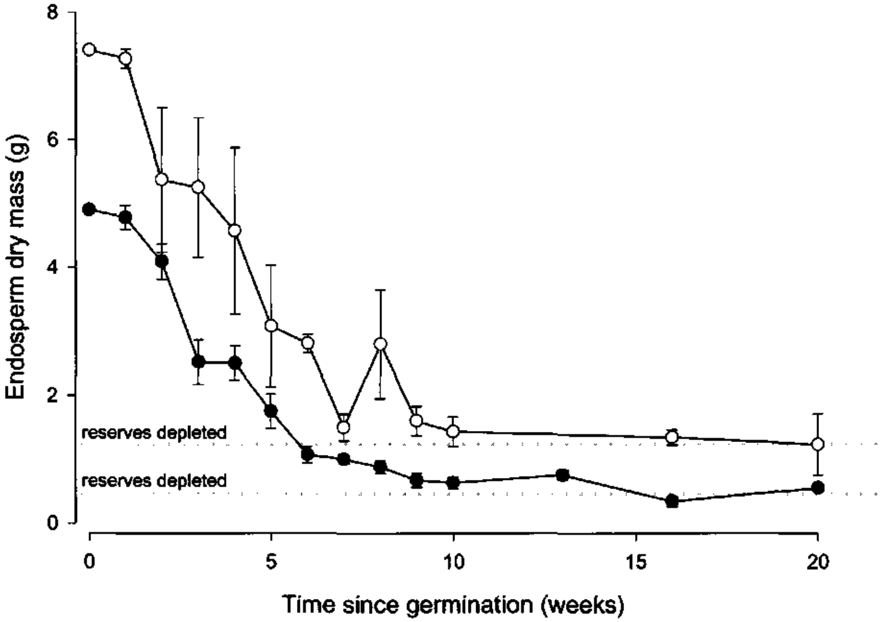

Figure 4.1 Depletion of seed reserves by germinating *Carapa procera* seedlings. Filled dots are small seeds (12.3 ± 1.2g fresh mass), open dots are larger seeds (20.7 ± 1.7g). Seedlings were grown on seed reserves only (perlite substrate without external nutrients). Greenhouse data, Wageningen, 1997.

especially acouchies (Jansen and Forget 2001). *Carapa* seeds, however, germinate rapidly under the moist conditions in the rainforest. Germinating seedlings fully deplete the seed reserves within two months, regardless of seed size (FIGURE 4.1). Thus, no seed reserves would be left by the time acouchies need their supplies, more than two months later.

4.2 Experiments and results

We monitored the fate of seeds cached by free-ranging acouchies during April – September 1999 at the Nouragues biological station, French Guiana. Feeding plots of 49 thread-marked seeds were established in each of 11 acouchy home ranges. Acouchy feeding behaviour and seed removal were recorded using video surveillance cameras. We subsequently located 314 acouchy-made caches by surveying the surrounding area for thread-marks protruding from the soil (FIGURE 4.2D). We then monitored cache depletion during 4 months.

We found that most seeds were recovered shortly after caching (93% within one month), well before the lean season. Few of these seeds, however, were eaten. The majority (c. 80%) was stored again in secondary caches. Video observations of feeding behaviour showed that acouchies extensively manipulate seeds before caching by taking them into their forepaws and smoothing the surface with their teeth (FIGURE 4.2A). Seeds recovered from caches to be re-cached were cleaned in the same way. Any irregularities such as protruding sprout, root and meristem were pruned (FIGURE 4.2B).

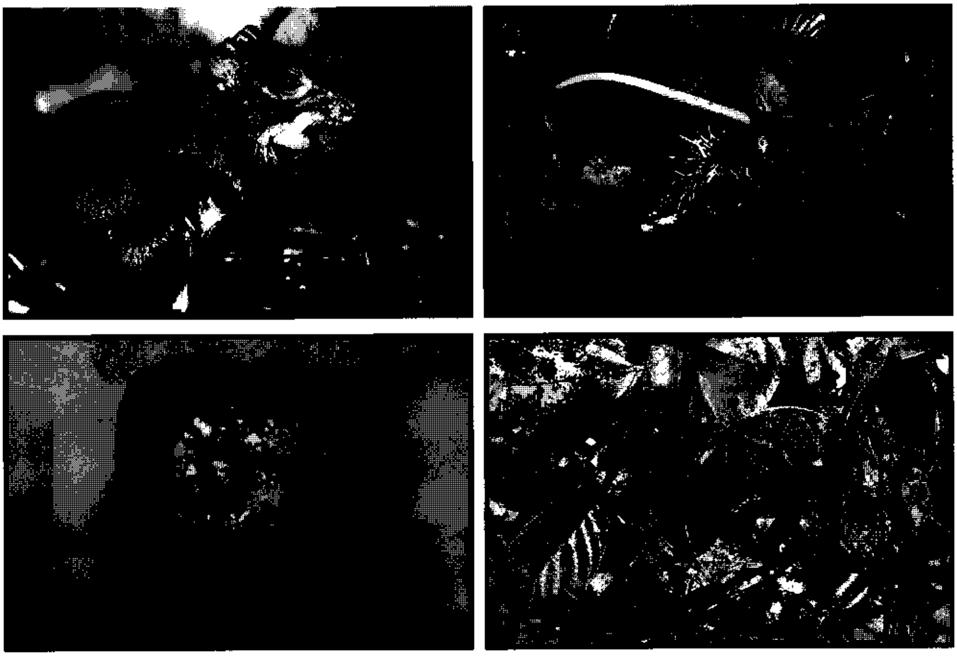

Figure 4.2 Green Acouchy (*Myoprocta pratti*) manipulating a seed (**a**); Depleted acouchy-made cache with severed *Carapa procera* shoot, root and meristem (**b**); *Carapa procera* 'zombie seed' with callus (**c**); Thread-mark giving away the hide of a cached seed (**d**).

We then experimentally tested whether pruning of seedling parts affected the seed's ability to resprout. We let 100 *Carapa* seeds of known fresh mass germinate during times varying from 0 to 28 days, severed the seedling, incubated the treated seeds in soil for times varying from 0 to 38 days, and then measured dry mass of seed parts. Seeds resprouted after removal of sprout and/or root, but no resprouting occurred after removal of the entire germ (i.e. everything protruding from the seed). Surprisingly, seed remains of the latter formed callus at the scar and then stayed alive and intact (FIGURE 4.2c), rather than dying and spoiling. Dry mass of callus increased with incubation time by *c.* 0.01 g day^{-1} (Linear regression: R^2=0.60, $F_{1,99}$=152), remaining negligible compared to endosperm dry mass. ANOVA showed that endosperm biomass was determined only by original seed fresh mass ($F_{1,96}$=47, P<0.001) and seedling growth time ($F_{1,96}$=17, P<0.001), and not affected by incubation time ($F_{1,96}$=0.2, P=0.666). While dead seeds normally decay within a few weeks under the moist rainforest conditions, endosperm biomass of treated seeds changed very little. We found endosperm that had still not completely decayed after ten months of burial.

We also tested whether the stage of germination at cleaning affected resprouting by experimentally removing the entire seedling at different stages of germination, from first appearance of the radicle to leaf formation. We severed the seedling from 118 seeds at different germination stages. After two weeks of incubation in soil, 114 seeds (97%) had formed a callus (FIGURE 4.2C) and one seed had resprouted. Three seeds were parasitized and spoiled. Seeds formed a callus regardless of germination stage.

We conclude that removal of a germinating seedling will almost always turn seeds into living dead – embryo-less seeds that stay physiologically active – with a dramatically increased endosperm storage life. Because the seeds continue living without purpose or physiological control by the embryo we refer to them as 'zombie seeds'.

Field data confirmed that the seed cleaning by acouchies turned germinating seeds into zombies. We tracked 194 thread-marked seeds in acouchy-made caches (FIGURE 4.2D) in the 2000 fruiting season and found that 76% of all seeds that were still cached after two months – mostly in secondary or tertiary caches – were zombie seeds. Of 86 seeds that were still cached after two months, 65 were zombies, 8% had become seedlings, and 16% had not yet germinated.

4.3 Discussion

Our findings show that hoarding rodents such as acouchies are capable of turning rapidly germinating and thus perishable *Carapa* seeds into a food with a long shelf life. Acouchies actively manage their seed supplies by recovering stored seeds once these germinate and prevent further seed reserve depletion. This type of management is an attractive explanation for the phenomenon of repeated re-caching, extending the existing idea of monitoring food quality and quantity (DeGange 1989). Similar seed manipulation has been observed in Grey Squirrels (*Sciurus carolinensis*) that excise embryos of White oak (*Quercus alba*) acorns to prevent autumn germination and assure an acorn food supply during winter (Fox 1982). The difference is that acorns treated by squirrels are killed but preserved by winter cold, while manipulated *Carapa* seeds are preserved alive in an environment of rapid decay.

We hypothesise that the phenomenon of zombie seeds is not restricted to *Carapa* and acouchies. Most forest ecosystems have scatterhoarding rodents as well as plant species with persistent seed reserves and protruding embryos. Tropical forest ecosystems, where life preservation of seeds is the only option, seem particularly rich in such seed. Cryptocotylars and hypogeals make up 21% of all species in tropical floras, and are frequent in common tropical plant families such as Dichapetalaceae, Legumunosae, Moraceae, Myristicaeae, and Sapindaceae (Garwood 1996). Rapid germination is also a common feature, especially among the large-seeded species that are interesting for hoarding animals (Rees 1996), and especially in tropical wet forests (Farnsworth 2000).

At first glance, the characteristic of becoming zombies after seed pruning seems a handicap to plants, since it may strongly reduce seed survival and, ultimately, plant reproductive success. However, scatterhoarding animals are important dispersal vectors for many large-seeded species (Vander Wall 1990; Jansen and Forget 2001). The plants' capacity of becoming zombies may actually be the only reason why scatterhoarding animals use these perishable seeds for long-term hoarding rather than instant consumption, and thus the only reason why they disperse them. If only a proportion of scatterhoarded seeds escapes the rodents' attention, dispersal success may already be sufficient (Jansen *et al.* 2002).

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5. The role of seed size in dispersal by a scatterhoarding rodent

5.1 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 with two extremes. 'Larderhoarders' store their food in one or few caches, each containing much food. 'Scatterhoarders', in contrast, store food by dispersing it in small amounts among many spatially separated caches. Where larderhoarding requires active defence or some other mechanism to prevent robbery of the food by competitors, scatterhoarding relies on spreading the risk of robbery (Vander Wall 1990). This chapter is about the long-term effects of scatterhoarding seeds in the upper layer of soil, as is practised by a variety of granivorous birds and mammals.

Scatterhoarding 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, scatterhoarding 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 seedeaters finding and killing the seed (Stapanian and Smith 1984; Vander Wall 1993) and often preserves seeds in better condition for germination and establishment (Vander Wall 2002).

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

Many plant species seem to depend on scatterhoarding 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 scatterhoarding peaks (e.g., Smythe 1970; Jackson 1981). These observations have lead to the hypothesis that these plant species are adapted to scatterhoarding: their reproductive strategy has been shaped by scatterhoarding animals over evolutionary time (Smythe 1970; Smith and Reichman 1984; Hallwachs 1994).

The adaptive explanation of the scatterhoarding 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 scatterhoarding animals in the temperate zone have indeed increased seed size since the Paleocene (~60 million years ago). Still, whether such increases occurred in response to scatterhoarding animals cannot be determined. What we can do, however, is test the underlying assumption that scatterhoarding 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 scatterhoarding animals could select for larger, more nutritious seeds, all of which assume it is more economical for scatterhoarders 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 scatterhoarders 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 (Waite and Reeve 1995). Thirdly, the decision of what to do with a seed after it is harvested may depend on seed value. Scatterhoarding animals usually eat a few seeds during the process of hoarding many others (Forget *et al.* 2002). The seeds they store may preferentially be high-value seeds, while low-value seeds are eaten (Hallwachs 1994). Fourthly, scatterhoarders 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. Scatterhoarders 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 scatterhoarders. We measured how seed value influenced the fate (death or establishment) of seeds offered to the red acouchy (*Myoprocta exilis*; Wayler 1831), a Neotropical rodent that scatterhoards seeds by burying them singly. A second aim was to quantify survival probabilities of seeds harvested and cached by acouchies, because direct proof for scatterhoarding 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.

5.2 Methods

Site and species

We worked at the Nouragues biological station in the Nouragues Reserve, an undisturbed lowland rainforest site in French Guiana, 100km south of the city of Cayenne, at 4°02' N and 52°42' W, and 100-150m above sea level. Annual precipitation averages 2900mm, 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 25m height, occurring throughout the Neotropics. *Carapa* produces up to 100 large (c. 10cm 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 (Forget *et al.* 2002). 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 (PHOTO 5.1), from less than 3g to as much as 65g (mean = ~21g).

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 scatterhoarding animal in French Guiana. It is a caviomorph rodent,

Photo 5.1 Seeds of the canopy tree *Carapa procera* (Meliaceae) cover a more than 20-fold range in seed mass, which makes this species excellent for use in seed size experiments.

33-39cm length, and weighs 1.0-1.5kg (Emmons and Feer 1990). Acouchies store seeds, their main food, by burying them in shallow caches in the topsoil. They are perfect scatterhoarders, because they harvest seeds one by one and store them in single-seeded caches. This behaviour led Morris (1962) to introduce the term scatterhoarding. Acouchies, like agoutis (*Dasyprocta*), scatterhoard 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 1ha (Dubost 1988).

Seed removal

Between 19 April and 24 May 1999, during the peak hoarding season, we established 11 feeding plots of 60 x 60cm below or near reproductive *Carapa* trees. Plots were separated by > 100m, 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 x 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 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 1m of fluorescent green fishing-line with 8cm 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 10m. 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 to 2 days after establishment of the plots. We attempted to retrieve all seeds, but stopped after 12 hours 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; Hoshizaki and Hulme 2002; Vander Wall 2002). 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 scatterhoarding 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

Photo 5.2 Video surveillance cameras were used to observe which animals removed individual seeds from the cafeteria plots.

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 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 timespan; 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

Table 5.1 Fates of *Carapa procera* seeds harvested by Red Acouchies (*Myoprocta exilis*) in French Guiana. The seed marked * had established a seedling at 4 months.

	Plot											Total
	1	2	3	4	5	6	7	8	9	10	11	
(a) Initial seed fate												
cached	40	23[a]	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 (*n*)	49	49	49	49	49	24[b]	49	49	37[b]	33[b,c]	49	486
(b) Initial fate of seeds recovered from primary caches												
re-cached	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[a]	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 (*n*)	40	23	37	23	17	4	39	44	20	23	34	304
half-life (days)	5	3	6	5	21	23	6	18	4	22	23	9
(c) 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[a]	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 (*n*)	49	49	49	49	49	24[b]	49	49	37[b]	36[b]	49	489

[a] includes one seed of unknown weight

[b] not including 50 seeds that were taken by peccaries or agoutis

[c] not including three seeds that were removed later than the first census

each plot: the regression coefficient β (or B) weighed by the inverse square of its standard error (SE),

$$\beta_i = \beta_i * SE_i^{-2} * \frac{1}{n}\sum_{i=1}^{n} SE_i^{-2}$$

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.

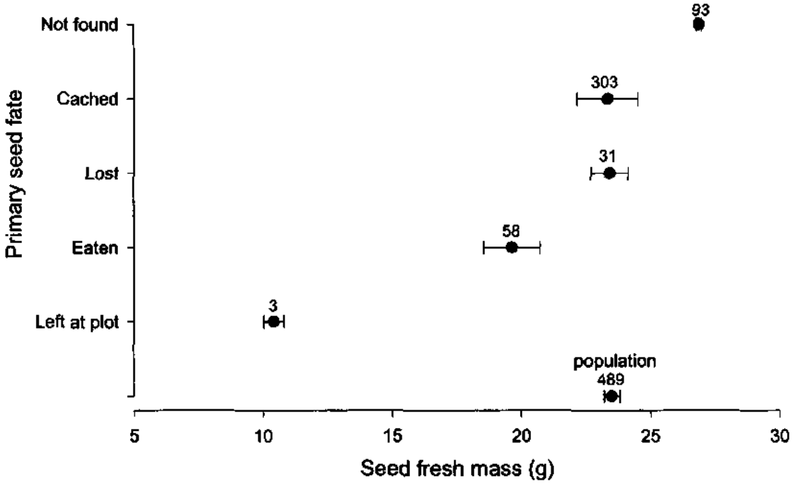

Figure 5.1 Effect of seed fresh mass on treatment of 488 *Carapa procera* seeds by Red acouchies (*Myoprocta exilis*). Data from 11 plots are pooled. Mean values (± s.e.) of seed fresh mass for different fates at one day after dispersal, and sample sizes. Seeds found eaten had lower masses (*t*-test: 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.

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).

5.3 Results

All seeds were removed within 1.5 days, except for three seeds, which were removed 1-2 days later (TABLE 5.1). 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 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 weighed linear

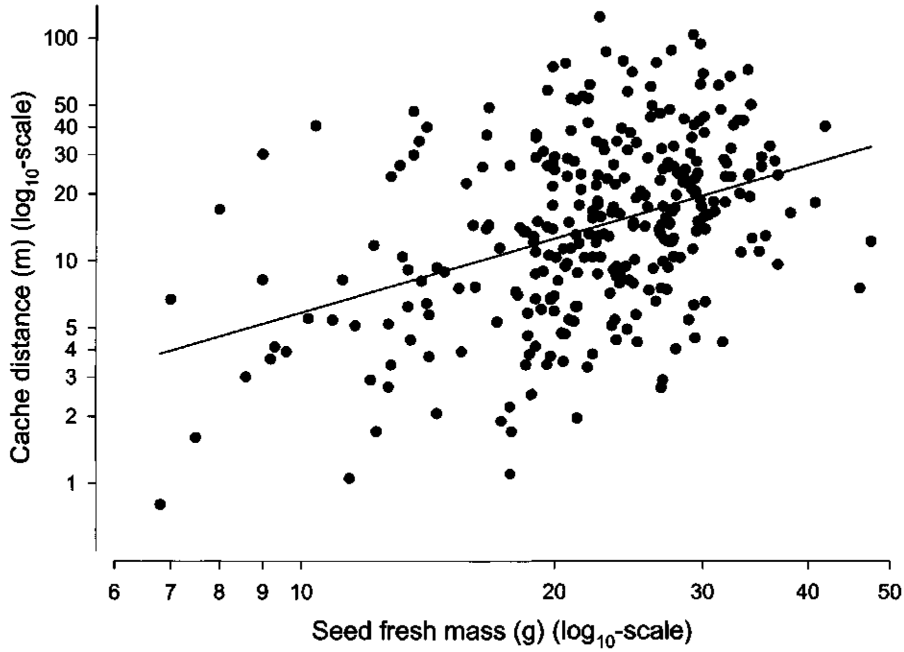

Figure 5.2 Effect of seed fresh mass on the distance from the source of acouchy caches found one day after dispersal ($\log_{10}$ scales). Pooled data (n=303) for 11 plots. Cache distance increased with seed fresh mass (ANCOVA: mass $F_{1,291}$=79, P<0.001; plot $F_{10,291}$=16, P<0.001; model $F_{11,291}$=22, R^2=0.45). The increase is significant at the plot level.

regression coefficients for 10 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=376, $F_{1,372}$=0.15, P=0.70). The animals spent little time selecting seeds (8 sec 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 5.1). The probability of being cached versus being eaten increased with seed mass at the population level, which confirms HYPOTHESIS 3 (FIGURE 5.1; 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.

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 <1m from the plot,

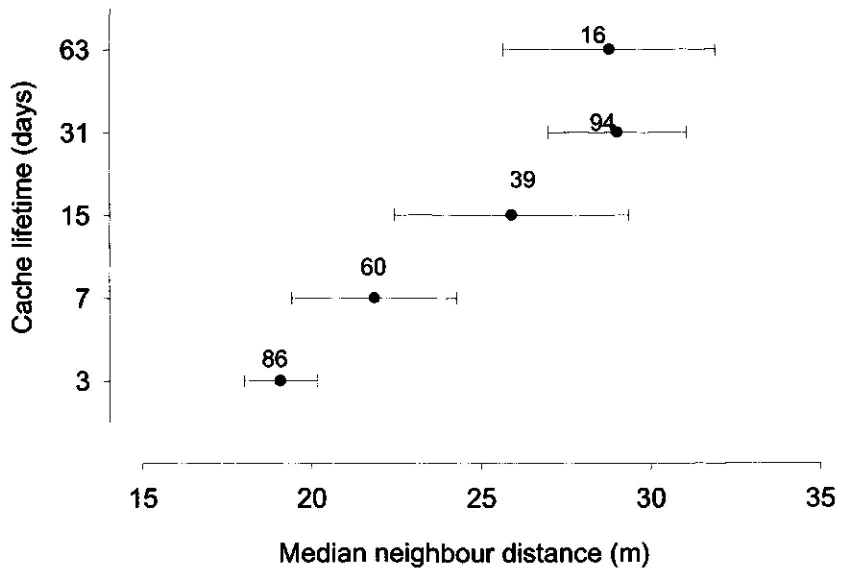

Figure 5.3 Effect of cache isolation (median distance to other caches) on cache lifetime, *i.e.* the time till a cache was found depleted (approximately on $\log_2$ scale). Pooled data (n=304) from 11 plots. Mean values (± s.e.) of isolation for different cache lifetimes, and sample sizes. Cache isolation positively affected the survival probability of caches.

the furthest was 124m away. Cache distance increased with seed size, as predicted by HYPOTHESIS 4 (t-test on weighed linear regression coefficients for 10 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 (FIGURE 5.2). 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 weighed linear regression coefficients for 10 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: $\beta_{distance}$=0.81, $F_{1,300}$=883, P<0.001; β_{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 (FIGURE 5.3; Cox regression: n=295 depleted, 9 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.

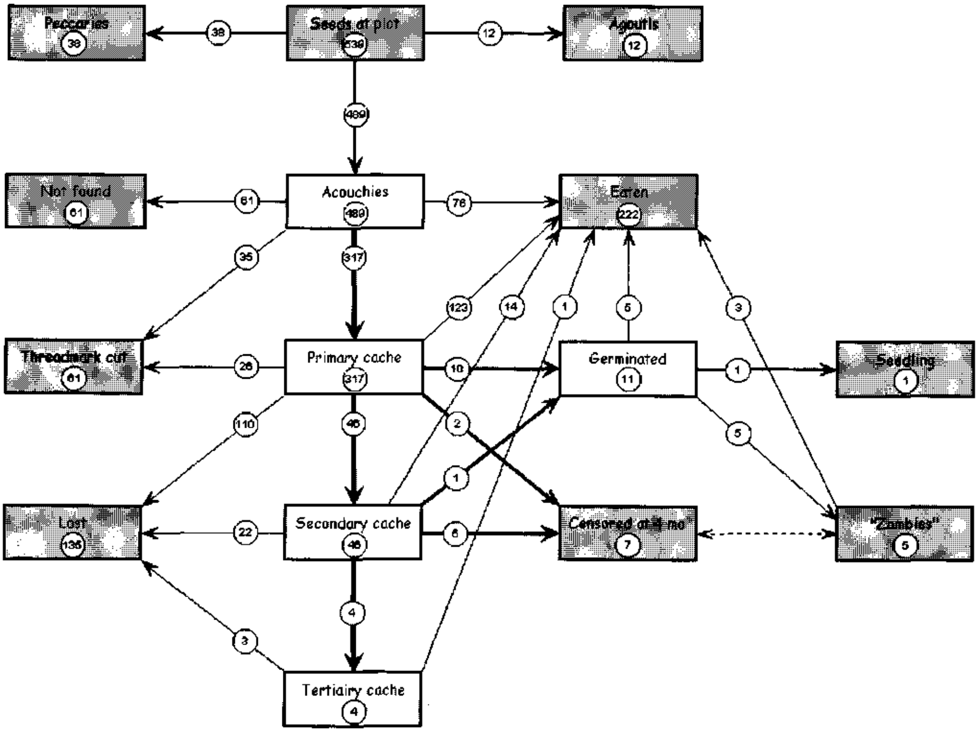

Figure 5.4 Fate pathways of 539 *Carapa procera* seeds placed in 11 plots in territories of different Red acouchies. Pooled data from 11 plots.

Recovery of seeds, however, did not necessarily lead to seed consumption. Many seeds were recached or were not found again (TABLE 5.1). 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 = 12m and 31m, 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, suggests that most of the seeds not found were actually recached at larger 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.

Ultimate seed fate

During subsequent searches and monitoring, we found additional seeds, mostly in caches at large 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 5.1). Of those, only one (0.5%) established a seedling. The remaining seeds were eaten (95%), had been displaced after germination and probably became

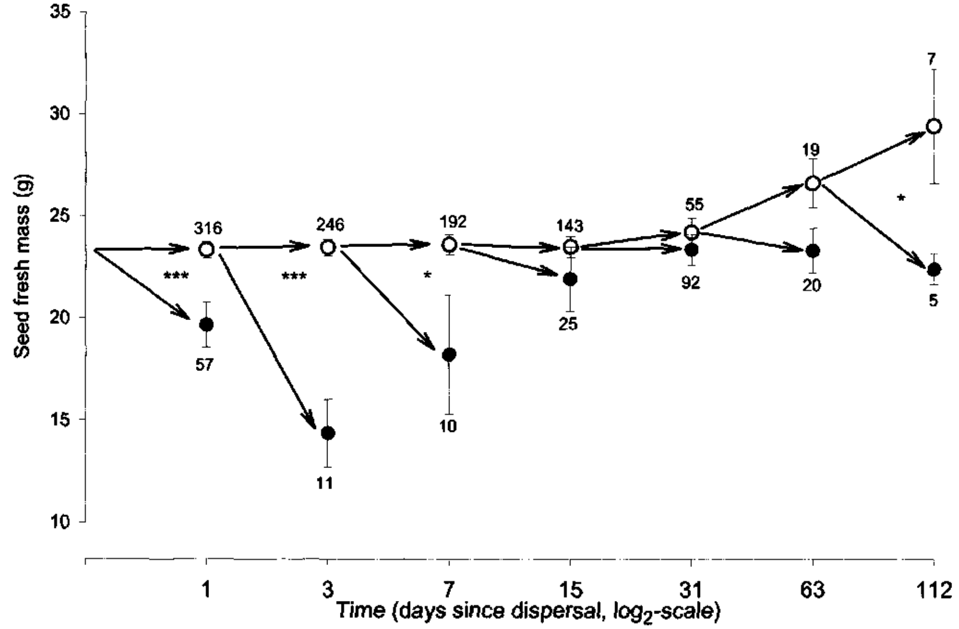

Figure 5.5 Change of mean mass of cached seeds over time (approximately on $\log_2$ scale). Pooled data from 11 plots. Filled circles are seeds that were found eaten at time t but still cached at time t-1, hollow circles are seeds that were still cached. Seeds that were taken from caches but not found 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, n.s. = not significant. Seed size increased the probability of* seeds remaining cached rather than being eaten.

'zombies' (1%) or were still cached without epicotyl (4%). Probably, the latter seeds had germinated and become 'zombies' without us noticing. Fates of all seeds are summarized in a seed-fate pathway diagram (FIGURE 5.4; 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 (FIGURE 5.5). 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 (FIGURE 5.6; t-test on weighed 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).

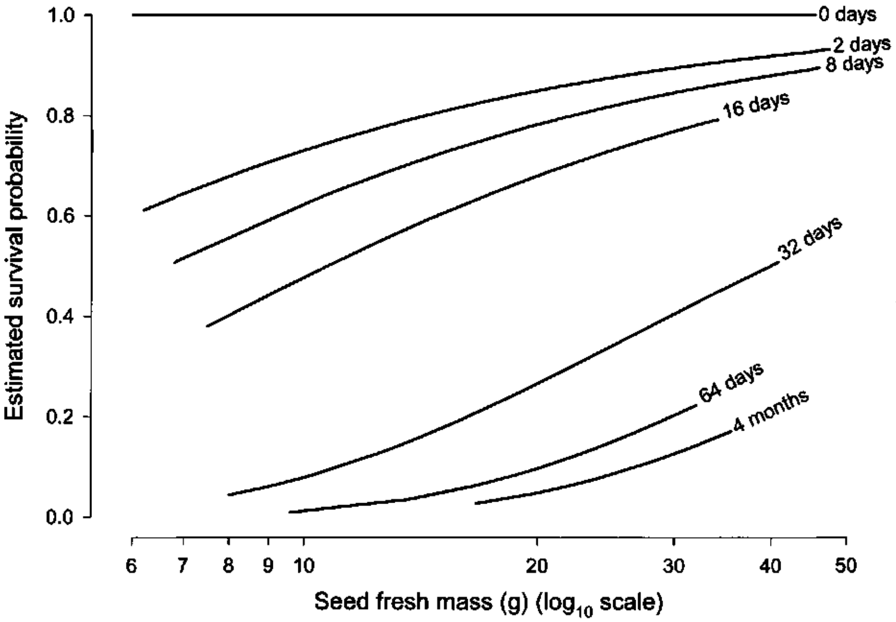

Figure 5.6 Effect of seed size ($\log_{10}$ scale) on seed lifetime. Survival probability curves as a function of seed mass according to the Cox regression model (see text for further explanation).

5.4 Discussion

The belief that many large-seeded tree species depend on scatterhoarding for regeneration has been largely based on the observation that scatterhoarding 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, 1995c, 2002; Hoshizaki and Hulme 2002). Our study is the first to determine ultimate seed fates of scatter-hoarded seeds in a tropical rainforest, with a known dispersal vector and over distances far beyond 50 m.

We found direct evidence that scatterhoarding 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 scatterhoarding. A more general idea of dispersal effectiveness requires estimations for more years, including both years with high and with low food availability.

Selection towards larger seeds

Our results indicate that scatterhoarding can result in selection towards larger seeds: the chance of surviving 4 months was negligible for small seeds compared to large ones. Larger seeds were more likely to be cached by acouchies rather than eaten (FIGURE 5.1) and were cached further away (FIGURE 5.2). Isolation of caches increased with cache distance and translated into longer cache lifetimes (FIGURE 5.3). If removed from their cache, larger seeds were also more likely to be re-cached than eaten. Overall, larger seeds were consumed at a lower rate than small seeds (FIGURE 5.5), which resulted in a higher net probability of survival and seedling establishment for large seeds (FIGURE 5.6). Seed mass, however, did not affect speed and probability of harvest by acouchies.

As was hypothesized by Smith and Reichman (1984), preference for large seeds by scatterhoarding 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 scatterhoarding 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 scatterhoarding 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 one 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

Scatterhoarding 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 ones and were more likely 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 size. All small acorns were eaten. Large seeds seem 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 larger 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 scatterhoarders hide higher-value food in lower densities (*i.e.* further away) to compensate for the greater risk of such food being robbed 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.

Table 5.2 Quantile regressions of cache distance on fresh weight for *Carapa procera* seeds scatterhoarded 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 weight (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 figure 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 (β_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

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 (FIGURE 5.2). 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 backward elimination of factors). We then calculated quantile regressions of cache distance on seed mass and on $\log_{10}$-transformed seed mass (TABLE 5.2). 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

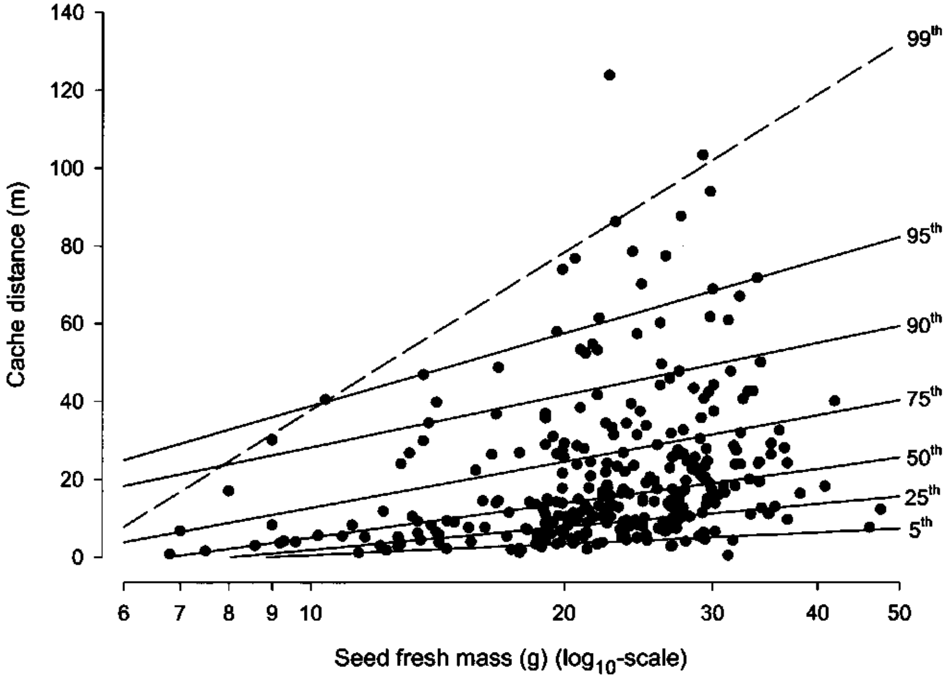

Figure 5.7 Effect of seed fresh mass ($\log_{10}$ scale) on the distance from the source of acouchy caches found one day after dispersal. Pooled data (n=303) for 11 plots. Plotted lines are significant quantile regressions for 7 values of τ (see TABLE 5.2).

the variation in distance occurs in the upper quantiles. Quantile regressions with seed mass $\log_{10}$-transformed gave the best fit (TABLE 5.2, FIGURE 5.7). 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 (1978). 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 scatterhoarding animals selects towards the production of large seeds. Scatterhoarding enables these plant species to produce larger seeds than species with other dispersal modes.

5.5 Acknowledgements

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6. Seed mass and mast seeding enhance dispersal by scatterhoarding rodents

6.1 Introduction

Scatterhoarding rodents and birds can play an important role in the seed-to-seedling phase of plants, both as consumers and dispersers of seeds (Chambers and MacMahon 1994; Price and Jenkins 1986). Evidence has recently accumulated that the net contribution of scatterhoarding to seedling recruitment in large-seeded plant species is positive (Vander Wall 2001 and references therein). The advantages to seeds of transport away from the parent plant, scattering over a large surface, and burial in the topsoil, can outweigh the disadvantage of a proportion of them being eaten during the caching process or after recovery from the caches. We have examples from all over the world of tree species exclusively depending on scatterhoarding rodents or birds for seed dispersal, including English Oak (*Quercus robur*) being dispersed by European Jay (*Garrulus glandarius*) in Europe (Bossema 1979), Japanese Horse Chestnut (*Aesculus turbinata*) by Large Japanese Field Mouse (*Apodemus speciosus*) in Asia (Hoshizaki *et al.* 1999), *Beilschemedia bancroftii* by White-tailed rat (*Uromys caudimaculatus*) in Australia (Theimer 2001), Black Walnut (*Juglans nigra*) by Fox squirrels (*Sciurus niger*) in North America (Stapanian and Smith 1978), and Brazilnut (*Bertholletia excelsa*) by Red-rumped Agouti (*Dasyprocta leporina*) in South America (Peres *et al.* 1997).

Scatterhoarder-dispersed tree species stand out by a seed production strategy that is remarkably different from that of functional groups with other dispersal modes in at least two ways. The first is large-seediness: seeds may be several orders of magnitude larger than those produced by tree species dispersed by wind or fruit-eating animals (e.g., Leishman *et al.* 1995; Westoby *et al.* 1996). The second is mast seeding. Populations of many scatterhoarder-dispersed tree species synchronously alternate abundant and reduced seed crops (Herrera *et al.* 1998; Vander Wall 2001). Nut-bearing tree species, which are typically scatterhoarded, tend to produce large seed crops at intervals of two to five years, with large and small nut crops differing in size by 2 or 3 orders of magnitude (Vander Wall 2001). The evolutionary significance of both seed mass and mast seeding are poorly understood and subject to debate. We studied seed fate in a Neotropical tree species dispersed by scatterhoarding animals to simultaneously investigate the role of seed mass and mast seeding for seed predation and dispersal.

Seed mass varies among plant species by ten orders of magnitude (Harper 1977). The question of why some species produce so much larger seeds than others has been addressed by many authors (e.g., Foster and Janson 1985; Grubb 1998; Kelly 1995; Westoby *et al.* 1992, 1996). Most consider seed mass as an evolutionary compromise between plant fecundity and dispersability on the one hand, selecting for small seeds, and seed vigor on the other, selecting for large seeds. Variation arises because species differ widely in the array of traits, habitat characteristics and evolutionary constraints that determine what seed mass is best. That dispersability decreases as seeds get larger, due to a lower ability or willingness of dispersal vectors to carry seeds, is one of the central paradigms in the seed mass debate (e.g., Baker 1972; Hedge *et al.* 1991; Howe and Westley 1986; Jordano 1995; Levey 1987; Mack 1993; Stanton 1984; Westoby *et al.* 1996). The more important dispersal is, the more a plant species would be limited in the size and, thus, the vigor of seeds it can produce. Moreover, because they are more interesting prey to seedeaters, large seeds would also suffer higher predation prior to dispersal (Janzen 1969, 1971).

Scatterhoarder-dispersed tree species challenge the generality of this idea (Jansen *et al.* 2002). In these species, large-seediness seems to stimulate rather than discourage dispersal by scatterhoarding animals. Several empirical studies have now shown that the probability of dispersal by scatterhoarding animals (Bossema 1979; Forget *et al.* 1998; Hallwachs 1994) and dispersal quality (Vander Wall 2003; but see Brewer 2001) may increase with seed size. Large seeds have a higher vigor and should therefore more likely germinate and establish a seedling once cached. However, large seeds may also be more likely recovered from caches as more valuable food items are more intensively sought after (Stapanian and Smith 1978) and possibly more easily discovered (Vander Wall 1993) by foraging animals. Scatterhoarders might recover and eat the largest seeds first to prevent these more valuable items from being stolen (Smith and Reichman 1984).

Almost as many papers have addressed the evolutionary ecology of mast seeding (e.g., Herrera *et al.* 1998; Ims 1990a; Kelly 1994; Koenig *et al.* 1994; Silvertown 1982). With the pollination efficiency hypothesis (Janzen 1967; Smith *et al.* 1990), the predator satiation hypothesis (Janzen 1970; Silvertown 1982) is the best-known functional explanation for the phenomenon (Kelly 1994). This hypothesis proposes that mast seeding is an evolutionary response to intense seed predation. By storing resources during some years, mast-seeding species can produce huge crops in other years (Sork 1993), which swamp local seedeaters with food and allow seeds to escape predation and successfully establish. Low seed crops in the intermittent years may prevent seedeaters from adapting their population levels (Janzen 1970). Plants producing large seed crops in synchrony with alike are predicted to experience less pre- en post-dispersal seed mortality and have disproportionally higher seedling recruitment than plants that produce non-synchronous seed crops (Ims 1990b; Janzen 1970). A lower percentage of predation in high seed years is a typical test for the predator satiation hypothesis (Kelly 1994).

Most empirical tests of predator satiation focus on pre-dispersal seed predation – the loss of seeds before a dispersal agent has manipulated it (Janzen 1971). The majority considers seed harvesting by seedeaters as pre-dispersal seed predation, backing up this assumption with observations of seed consumption (e.g., Boucher 1981; Kelly 1994). In many nut-bearing species, however, these seedeaters also function as seed dispersers. More strongly, seedling establishment requires that these animals harvest and subsequently scatterhoard seeds, and relies on the animals imperfectly recovering their caches. Thus, the function of predator satiation would be to stimulate scatterhoarding seedeaters acting more as dispersers and less as predators of the seeds they harvest. The animals store seeds far in excess of what they can ever recover and eat, thus allowing many dispersed seeds to germinate and establish (Vander Wall 2001). Although no more than a special case of the predator satiation hypothesis, this effect is sometimes referred to as the 'animal dispersal hypothesis' (Kelly 1994; Vander Wall 2003).

An alternative hypothesis that has received far less support is the 'large seed size hypothesis', which is based on the observation that inter-mast intervals of oaks tend to increase with seed mass (Sork 1993). It proposes that selection towards larger seeds indirectly increase the contrast between high and low seed years, because the production of large seeds requires accumulation of resources during a longer period of time (Kelly 1994; Sork 1993). Thus, mast-fruiting species store resources during some years in order to produce large-seeded crops in others. So far, the large seed size hypothesis has been related to habitat requirements and seedling vigor selecting for large seeds (Sork 1993 and references therein), while 'seed predation' was assumed to select against large seeds (Janzen 1969; Sork 1993). As explained above, dispersal by scatterhoarding animals may also select for large seeds, and we are especially interested in the combined effect of seed mass and seed abundance on scatterhoarding. As a matter of fact, Kelly (1994) put forward that the large seed size hypothesis cannot alone explain mast seeding. It implicitly requires some other factor to determine a minimum number of seeds per crop, with predator satiation as again the best candidate. The two factors combined could explain why nut-bearing seeds are large and numerous at the same time, and could reinforce each other (Kelly 1994; Sork 1993).

Both seed mass and seed abundance are aspects of seed economical value. The seed nutritional content represents the absolute value, whereas seed scarcity sets the value of seeds as perceived by seedeating animals. The scarcer seeds are, the more valuable seed items will become. It is plausible that seed mass and seed abundance aspects interact. Foraging theory predicts that scatterhoaders will preferentially harvest the most valuable seeds, *i.e.* the largest, most nutritious seeds. However, animals may not afford this luxury when seed is scarce and they need every single seed they can find to build sufficient stock for surviving. Thus, seed abundance could enhance the positive effect of seed mass on dispersal success. Large seeds having greater dispersal success makes sense in the light of foraging theory (Stephens and Krebs 1986), because large seeds of the same species have a higher nutritional value (Grubb and Burslem 1998). Optimal cache spacing theory (Clarkson *et al.* 1986; Stapanian and Smith 1978) argues that scatterhoarders can increase the net energy benefit of caching, given fixed handling costs, by focussing on large seeds. However, a higher nutritional value may also increase the motivation of food competitors to search for caches. Scatterhoarders must anticipate by better caching, *i.e.* further away and in lower densities, reducing the probability of cache robbery. It is this better caching of large seeds that can subsequently translate into a greater probability of large seeds not being recovered and escaping consumption (CHAPTER 5). Thus, large seeds can acquire a greater ultimate probability of seedling establishment, even though they are the most valuable seeds to seedeaters.

The prediction of greater dispersal success under fruit abundance, however, is to some degree contra-intuitive. Foraging theory predicts that the per-capita probability of seeds being harvested and scatterhoarded is maximal under seed scarcity. Likewise, the quality of scatterhoarding (*i.e.* distance, density and depth of caches) should also be higher under food scarcity, as scatterhoarders anticipate the high motivation of food competitors to search for scarce seeds. What does make sense is that seed abundance should increase the probability of cached seeds escaping consumption and establishing a seedling. Cached seeds are not likely recovered as long as non-cached seeds are plenty, and caches are so abundant that the per capita probability of ultimately being recovered is low. Thus, seeds only have a greater probability of establishing under seed abundance if the benefit of low cache recovery under seed abundance outweighs the benefit of good scatterhoarding under seed scarcity.

This study

We tested the idea of large-seediness and synchronized mast seeding being adaptations reducing seed predation and enhancing effective seed dispersal. Moreover, we tested the idea that seed mass and mast seeding interact positively. We studied the effectiveness of seed dispersal by scatterhoarding rodents in a Neotropical rainforest by tracking the fates of individual seeds of varying seed mass in two years of seed scarcity and three years of seed abundance. Henceforth, we shall refer to these as 'poor years' and 'rich years', respectively (*cf.* Kelly 1994). We evaluate the community-wide availability of large seeds, rather than the availability of a single masting species. Seed fate is influenced by the availability of other seed species (Hoshizaki and Humle 2002), and nut-bearing species need not produce large crops in synchrony with other species (Vander Wall 2001). The present study compares the success of seeds that are produced in and out of synchrony with community-wide seed set. Kelly (1994) advocated this approach as one of the most promising.

Successful dispersal by scatterhoarding animals has three key elements: (i) seeds are taken away from below the parent rapidly, before they deteriorate (e.g., due to insects or fungi), germinate in the wrong place, or be found by non-hoarding granivores; (ii) seeds are subsequently scatterhoarded. The further away from the parent and the lower the density, the better; (iii) cached seeds are left undisturbed by seedeaters as soon as germination sets off, until seedling establishment and complete depletion of seed reserves. Being harvested (i) is important because the per capita probability of recruitment in the direct vicinity of the parent tree is extremely low. Parent and siblings already occupy the place and the risk of parent-associated or density-dependent mortality is high.

Dispersal before germination (i) and rest after germination (iii) are important because rodents cut protruding germs when handling germinated seeds. This treatment not only sets back germination but can also destroy the seed's ability of sprouting (CHAPTER 4). Dispersal and isolation from conspecifics (ii) are needed to get away from the vicinity of the parent tree, increase the likelihood of colonizing new sites, and reduce density-dependent seed predation, especially by naïve foragers searching for cached seeds (Stapanian and Smith 1978). Dispersal by scatterhoarders (ii) comes with burial, which enhances successful seedling establishment (Vander Wall 1990).

The set of hypotheses that we tested, shown in TABLE 6.1, summarizes as follows:
(1) Seed mass increases dispersal effectiveness: it enhances dispersal in all phases;
(2) Seed abundance increases dispersal effectiveness: high survival of cached seeds outweighs negative effects of food abundance in all other dispersal phases, and;
(3) Seed abundance reinforces the positive effect of seed mass on dispersal effectiveness. All predictions in TABLE 6.1 are based on optimal foraging and optimal cache spacing predictions: (a) rodents preferentially harvest and stock the most nutritious seeds; (b) rodents spend a more effort on caching such seeds; (c) seed abundance increases rodent selectivity, and; (d) seed abundance decreases the effort rodents spend on caching and cache management.

Table 6.1 Hypotheses on the effect of seed mass, seed abundance an their interaction on different phases of seed dispersal and seedling establishment. See SECTION 6.1 for explanation.

	Indicator	**effect of abundance** rich vs lean years (a)	**effect of mass** large vs small seeds (b)	**interaction** effect of seed mass (c)
1	seed harvesting	slower harvesting	faster harvesting	greater in rich years
2	caching | harvest	less caching	more caching	greater in rich years
3	1st dispersal | caching	lower dispersal	further dispersal	greater in lean years
4	cache recovery	slower recovery	slower recovery	greater in lean years
5	re-caching | recovery	less re-caching	more re-caching	greater in rich years
6	2nd dispersal | re-caching	lower dispersal	further dispersal	greater in lean years
7	seedling establishment	more establishment	more establishment	greater in rich years

6.2 Methods

Site and species

This study was carried out at the Nouragues biological station, an undisturbed tropical lowland rainforest site in French Guiana, 100km south of Cayenne, at 4°02' N and 52°42' W, and 100-150m above sea level. Annual precipitation averages 2900mm, 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.

The tree species used in this study was *Carapa procera* (Meliaceae), henceforth Carapa, a lower canopy tree of ~30m maximum height that is frequent in parts of the Guianas and the Amazon. Trees produce globoid 5-valved dry fruits, each containing up to 20 large, fatty seeds of 21g average fresh mass (Jansen and Forget 2001). In April – May, during the wet season, fruits dehisce in the tree or burst when falling on the ground, and seeds scatter over the forest floor. Seeds that are not removed from below parent trees are subject to infestation by *Hypsipila* moths. *Carapa* tends to 'putative masting' (*sensu* Kelly 1994), meaning that seed crops vary greatly between years, but there is no strong bimodality in crop sizes. In our study period, rich crops of *Carapa* coincided with seed set of the two other important large-seeded, rodent-dispersed species in the study area: *Vouacapoua americana* (Caesalpiniaceae) and *Licania alba* (Chrysobalanaceae), which have normal masting (*sensu* Kelly 1994). Thus, community-wide availability of nuts showed a clear dichotomy of poor and rich years.

Carapa is an ideal species for our study, for three reasons. First, horizontal seed dispersal is exclusively by terrestrial scatterhoarding rodents, which greatly facilitates seed tracking. Second, fresh masses of ripe seeds span a more than 20-fold range, from less than 3g to more than 60g. This allows us to vary seed mass within a single species, thus avoiding confounding factors that make comparative studies of seed mass difficult to

Table 6.2 Data collected for this study.

	Rich years				Lean years			Total
	1996	1998	2000	Total	1997	1999	Total	
No. of seed plots	36	5	10	51	30	11	41	92
No. of recordings	5	4	10	19	29	11	40	59
No. of seeds	900	245	490	1,635	725	539	1,264	2,899
Plot size	25	49	49		25	49		
Harvesting and hoarding	+	+	+	1,635	+	+	1,264	2,899
Primary cache survival	-	-	+	490	+	+	1,264	1,754
Ultimate seed fate	-	-	+	490	-	+	539	1,029

interpret (Hurly and Robertson 1987). Third, although seed production by the *Carapa* population varies greatly between years, the species produces at least some seeds every year. Thus, we had the same fresh seeds available in both rich and poor years. The drawback of the latter is that we are testing hypotheses on the advantage of mast seeding using a non-masting species for which this advantage may be non-existing. We solved this problem in our analyses by playing apart general trends in scatterhoarder responses on the one hand, and effects of *Carapa* characteristics, such as rapid germination and rapid decay of exposed seeds, on the other (see analysis section).

The principal dispersers of *Carapa* and other large-seeded plant species in French Guiana are the Red acouchy (*Myoprocta acouchy*) and the Red-rumped agouti (*Dasyprocta leporina*). Both scatterhoarding rodents harvest seeds one by one and bury them in spatially scattered single-seeded caches in litter or topsoil (Forget 1990, 1996; Jansen *et al.* 2002; Jansen and Forget 2001; Morris 1962; Smythe 1978). The cached seeds are drawn upon as food reserves in the period of low fruiting following hoarding (Henry 1999), but some seeds are never used and establish seedlings. Important seedeating mammals without dispersal function are Collared peccary (*Pecari tajacu*) and White-lipped peccary (*Tayassu pecari*) that instantly consume seeds they encounter, crushing and killing all large seeds. Peccary herds also search for cached seeds (Kiltie 1981), which is believed to force rodents to space out seeds as much as possible.

Experiments

The fieldwork was carried during the wet seasons of 1996-2000. This period included three rich seed years (1996, 1998 and 2000) and two poor seed years (1997 and 1999). Rich years had more or less abundant fruiting of *Carapa*, mast seeding *Vouacapoua americana* and *Licania alba*, and fruiting by many other species. Poor years had modest fruiting of *Carapa* and few other species, but not *Vouacapoua* and *Licania*. The data come from 87 experimental seed plots that we established in the understorey throughout the Nouragues area, roughly half of them in rich years, half of them in poor years (Table 6.2) during 2½ months (Early April to Mid June). This period is characterized by intense hoarding activity (Forget 1996; Forget *et al.* 2002). At all plots we monitored removal and scatterhoarding, at a subset of them we also measured cache survival and ultimate seed fate. Thus, we obtained data on seed harvesting and scatterhoarding for 87 plots (*ca.*

2,654 seeds over 4 years), cache survival for 51 plots (1,754 seeds over 3 years), and ultimate seed fate for 21 plots (*ca.* 1,029 seeds over 2 years). The amount of seeds per plot varied between years, but the overall structure of the data collected was roughly balanced between poor and rich years (TABLE 6.2). All plots were established between early April and early June, which covers the period of maximum hoarding activity as well as the period of fruit production by typical rodent-dispersed species.

Each seed plot consisted of 25 (in 1996-1998) or 49 (in 1998-2000) fresh seeds in a 5x5 or 7x7 grid, respectively, with 9-12cm between seeds. 75 plots (2,354 seeds) each contained a large continuous range of seed fresh mass, on average 8-40g or a half order of magnitude. The mass range was created by stratified seed collection from the local *Carapa* population. In this way, we controlled for any effect of seed mass on the probability of discovery: an animal visiting a seed plot discovered all seed masses at the same time and had to choose. The 1997 sample also included 4 plots (100 seeds) with a single seed mass, and 8 plots (200 seeds) with two contrasting seed masses. All seeds were thread-marked (*cf.* Forget 1990) with 1m fluorescent green fishing line attached to the seed by piercing. Thread-marks enabled retrieval of cached seeds, as the rodents bury the seeds but leave the threadmarks protruding from the soil. To further facilitate tracking of dispersed seeds, we added 10cm of pink-fluorescent flagging tape (Forestry suppliers) at the end the thread in 1999 and 2000. Seeds were numbered individually by a barcode on the end of the thread or by a number on the flagging. We chose to accept possible side effects of piercing, such as more rapid infestation or germination, assuming that such effects would be independent of the target variables of seed mass and seed abundance.

A subset of plots was video-observed for several hours up to several days (depending on the speed of seed removal and available power). This subset also included four seed plots from 1998 for which we have no further seed fate data. We used a monochrome CCD video surveillance camera (Philips VCM 6250/00T) in a waterproof housing (VT VHL-2EC) and a 12V time lapse video recorder (Panasonic AG-1070 DC), powered by a 12V car battery. We mounted the camera on a tree at ~1.5 m, and hung up the recorder 2-3m away in a waterproof bag and netting. Recording was either continuous at 4 frames s^{-1} or non-continuous at 16 frames s^{-1} triggered by a passive infrared sensor detecting movement (ASIM IR 207). Date and exact time were also recorded. In 1996 and 1997, we also recorded at night, lighting the plots with an infrared lamp (Dennard 880M20). When the recordings showed that nocturnal seed removal (e.g., by paca, *Agouti paca*, or spiny rats, *Proecimys* spp.) was rare, we decided to invest all power in recording diurnal seed removal.

Seed harvesting

We measured the rate of seed harvesting by monitoring removal of individual seeds from plots. This was done at approximately 1, 2, 4, 8, 16, 32, 64 and 128 days (corresponding to a 2^n-scale), sometimes with additional days in between. When video data were available, we determined the identity of animals removing individual seeds, as well as the exact time and order of seed removal during the first time. We also used the video data to estimate how much time long it took for seed plots to be discovered (*i.e.* first visited) by Red acouchy (*Myoprocta exilis*), Red-rumped agouti (*Dasyprocta leporina*), peccaries (*Tayassu tajassu* and *T. pecari*) and Guianan red squirrels (*Sciurus aesthuans*).

If seed removal was slow, seed germination, infestation by insects and/or infestation by fungi occurred, in any order. Since these likely affected the attractiveness of seeds for mammals, we also recorded these intermediate events. Moreover, rodents sever the seedling when harvesting germinated seeds, which turns seeds into 'zombies'; seeds that are still alive, *i.e.* physiologically active, but technically dead because they lost their ability to sprout (CHAPTER 4). We calculated (1) time till germination; (2) time till visible infestation; (3) time till fungal attack; and (4) time till removal. We timed parasitism, fungal attack and removal at the middle of a monitoring interval. Time of germination was estimated by considering the germination stage. Data were right-censored at the end of monitoring if a given event was not observed.

Scatterhoarding

We studied scatterhoarding at two third of the experimental plots by thoroughly surveying a circular area for thread-marked seeds. At half of the plots we searched 10m or further, at a quarter of them 25m or further. Beyond this radius, we often did directional searching to include large dispersal distances. Searching was done once at least 75% of the seeds had been removed or one week had elapsed. For each seed retrieved, we recorded whether it was consumed or scatterhoarded, and measured distance and direction from the source. For each seed we calculated the median distance to neighboring caches from the same plot, and used this value as a measure of cache isolation (*i.e.* the inverse of density). Median neighbor distance is strongly correlated to nearest neighbor distance, but more robust to caches being overlooked, for example when the threadmark is bitten off.

We retrieved only 55% of harvested seeds. We have several reasons to think that these samples were biased against large seeds, cached at greater dispersal distances. We recorded several dispersal events over distances greater than 100m, suggesting that many seeds will have been dispersed beyond our search radius. Seeds that were indeed dispersed beyond our search radius were more likely cached than eaten, as seed consumption tended to be close to the plots. Most consumed seeds were found at or near to the cafeteria plot. Moreover, among seeds retrieved beyond 10m shortly after dispersal, consumed seeds were rare. Finally, non-retrieved seeds tended to be heavier than seeds found cached, which suggests that large seeds were more likely dispersed beyond our search radius than small seeds.

Cache survival and seedling establishment

We measured cache lifetime by monitoring caches at least at 2, 4, 8, 16, 32 and 64 days after seed removal (corresponding to a 2^n-scale). We also recorded germination by checking for seedlings emerging from caches and severed sprouts next to depleted caches. In 1999 and 2000, we also measured the ultimate fate of seeds by tracking them until they had died, had established a seedling, or had become 'zombies'. We attempted to relocate seeds that had been removed from caches and record their status by repeating the area survey at 32 and 64 days. As with removal, we timed parasitism, fungal attack and recovery at the middle of a monitoring interval, and estimated time of germination by considering the germination stage. In 2000, we also dug up all cached seeds remaining at the end of monitoring and recorded their status.

Statistical analyses

Our seed fate study yielded complicated data on seed fate pathways from seed to established seedling or death. We used the counting process notation (Andersen *et al.* 1993) to record successions of events – such as germination, harvesting, caching, cache recovery, re-caching and consumption – that happened for individual seeds. We then split these 'event histories' into six seed fate processes: (A) seed harvesting from cafeteria plots, (B) seed caching versus consumption after harvest, (C) primary dispersal distance given caching, (D) seed harvesting from caches, (E) seed re-caching versus consumption after cache depletion, and (F) secondary dispersal distance given re-caching. Processes D-F include primary, secondary and tertiary caches. For each seed fate process, we analyzed the explanatory value two main effects - seed mass and seed abundance - and time. To play these effects apart, we developed statistical models for each partial fate, in which we accounted for event history and other confounding factors. The fitted models quantify the direct contribution of seed mass and seed abundance to seed fate in the different life phases.

Descriptive statistics

Typically, seed fate data are series of events – 'failures' – that happen after the elapse of time – 'failure time'. We used different survival analysis techniques to analyze the failure times in our study: time-till-discovery of plots, time-till-harvest of seeds from plots, and time-till-recovery of seeds from caches. An attractive characteristic of survival analyses is that they allow for the inclusion of censored cases: cases in which the event of interest is not recorded during the observation time. Although we do not know the exact failure time of such cases, we do know that the failure time exceeded the observation time, and including this information is crucial. Events were defined as selection of a seed by a granivorous mammal (or first visitation of a plot), regardless of the subsequently fate. Video recordings yielded exact failure times. Other failure times were set between the last census time at which an event had not yet taken place and the first census time at which it had. Because our monitoring schedule became increasingly course over time, failure times were less accurate as events happened longer after plot establishment.

We described seed harvesting from plots (A), including the discovery of plots, and seed recovery from caches (D) using the Kaplan Meier (KM) estimate of survival. The KM-estimate is a product of survival probabilities:

$$\hat{S}KM(t) = \prod_{t_i<t} \frac{r(t_i)-d(t_i)}{r(t_i)}$$

in which r is the number of seeds at risk (waiting for an event to happen) and d is the total number of events that happened at time t_i. The resulting survival curve is a step function that ranges from 1 to 0 with a drop at each event. We show 100 x (1-$\hat{S}$KM(t)), the cumulative percentage of individuals for which the event took place. The Mantel-Haenszel or log-rank test was used to statistically compare survival curves between rich and poor years. We used the median failure time – the time at which the $\hat{S}$KM(*t*) equaled 0.5 (*i.e.*, the seeds' 'half-life') – as indicator of the speed at which events took place, as a function of seed mass in rich and poor years.

Post-harvest seed fate (B) and post-recovery seed fate (D) were binary data: seeds were either eaten or (re-)cached. We used logistic regression to analyze alternative fates as a function of seed mass in rich and poor years. The logistic model describes the probability P(X) of a seed having fate D as an S-shaped function ranging between 0 to 1:

$$P(X) = P(D = 1 \mid X_1, X_2, \ldots, X_k) = \frac{1}{1 + e^{-(\alpha + \Sigma\beta_i X_i)}}$$

in which β_i is the coefficient of covariate X_i, and α is the coefficient describing the background variation. The adjusted odds ratio, e^{β_i}, indicates the effect on P(X) of one unit increase of variable X_i adjusted for the other covariates. We used the Wald statistic – the square of the coefficient estimate divided by its standard error, which is distributed as χ^2 – for significance testing. The processes C and F (primary and secondary dispersal distance) were described using linear regression.

Cache distance and seed fresh mass were ln(*x*+1)-transformed in all analyses. Thus, we consider the relative increase in dispersal distance and seed mass rather than the absolute increase. Analyses were done using SPSS 10.0.5 (SPSS 1999).

Model fitting

Many factors other than seed mass and seed abundance potentially influenced the fate of seeds in each process. These include differences in experimental set-up as well as differences in event history, *i.e.* what happened to seeds in previous processes or during a process. Generalization of the results and evaluation of ultimate cumulative effects required that we accounted these factors. Therefore, we statistically modeled the effects of the main factors seed mass, seed abundance and their interaction, while incorporating other variables that likely influenced seed fate.

We accounted for six such possible effects: (a) seasonal effects. The experiments covered a 4 months season during which seed availability tends to decline, while the lean season is approaching. Therefore, the time at which a process started likely influenced the foraging behavior of seedeaters and therefore seed fate. We defined time as the number of days elapsed between start of a process and April 7th. This is the earliest date our sample, as well as the approximate time at which both nut production and scatterhoarding start off (*cf.* Forget 1996, 2002); (b) dispersal distance. Far-dispersed seeds are in lower densities and thus less prone to density-dependent mortality regardless their size; (c) experimental layout. Differences in site and the number of seeds between plots likely influenced the rate of seed harvesting and the fate of harvested seeds. Because our set-up was not completely balanced, we had to control for these effects; (d) species-specific effects. *Carapa*'s early germination and the vulnerability of exposed seeds to insect attack and desiccation likely influence seed fate. We must control for these internal effects to quantify the general, external trends; (e) search bias. Retrieval of seeds after dispersal is never complete. This is the more problematic when the retrieved seeds are not random subset of the total population; (f) inter-dependence of seed fates. We treated seeds as experimental units, reasoning that the seed plots in our study are more numerous than the seeds within every plot. However, the harvesting rate and fate of seeds within the same plot were likely correlated. Therefore, we had to make sure that the observed effects were not due to deviant plots or animals.

Models were fitted using a stepwise backward elimination procedure with Akaike's (1978) Bayesian Information Criterion (BIC). According to this criterion, the 'best model' *m* has the lowest value of

$$BIC_m = -2\,Ln(L_m) + \ln(n)\cdot k_m,$$

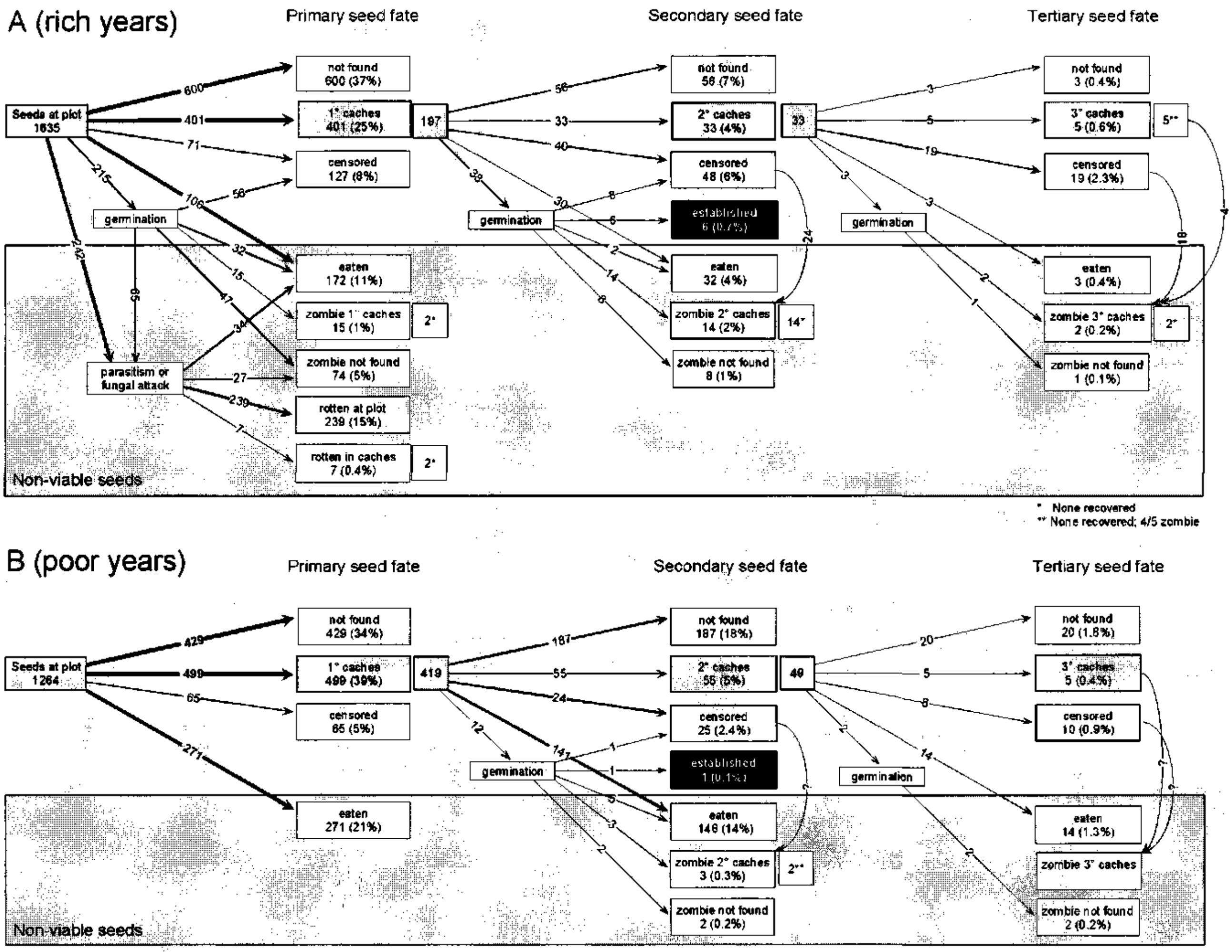
where L_m is the sample log-likelihood for the m^{th} of M alternative models and k_m is the number of independent parameters estimated for the m^{th} model. The term ln(*n*) is a penalty for over-parameterization, that increases with sample size. Seed removal and cache recovery (the processes A and D) were analyzed using the Cox proportional hazards model (Cox regression). The Cox model is written as:

$$h(t,X) = h(t,X_1,X_2,\ldots,X_k) = \varpi_j \cdot h_0(t)\cdot e^{\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k},$$

in which $h_0(t)$ is the baseline hazard: the probability of harvesting / recovery over time for a seed with all variables set to zero. The exponential is the proportional increase of this probability by the explanatory variables X_i. The coefficients β_i describe the contribution of each individual variable. As in logistic regression, the effect of one unit increase of variable X_i adjusted for the other covariates, is described by e^{β_i}, the hazard ratio. We used the Wald statistic for significance testing. The parameter ϖ_j in the Cox model is a frailty term, describing an unobservable random effect shared by seeds from the same plot. By adding this frailty to the fitted model for seed harvesting, we checked whether and how interdependence of seed fates within plots affected the parameters of our fitted models. The frailty approach is commonly used in pharmaceutical trails to correct for possible effects of kinship in laboratory animals. Post-harvesting and post-recovery seed fate (the processes B and E) were analyzed using logistic regression models (see above). We accounted for the search bias (see below) by treating non-retrieved seeds as seeds cached beyond the search radius, given that the search radius exceeded 10m (process B) or 5m (process D).

Table 6.3 Numbers of *Carapa* seeds harvested by seed-eating mammals in rich and poor years, and their subsequent fate (primary seed fate in FIGURE 6.1).

			Primary seed fate					
Species	No. of seeds		eaten (%)		cached (%)		unknown (%)	
Poor years								
Acouchy	727	(58%)	75	(10%)	376	(52%)	276	(38%)
Agouti	33	(3%)	5	(15%)	2	(6%)	26	(79%)
Peccary	124	(10%)	124	(100%)	-		-	
Unknown	315	(25%)	67	(21%)	121	(38%)	127	(40%)
Total harvested	1199		271	(23%)	499	(42%)	429	(36%)
Rich years								
Acouchy	157	(10%)	12	(8%)	117	(75%)	28	(18%)
Agouti	0	(0%)	-		-		-	
Peccary	0	(0%)	-		-		-	
Unknown	1112	(68%)	160	(14%)	306	(28%)	646	(58%)
Total harvested	1269		172	(14%)	423	(33%)	674	(53%)



* None recovered
** None recovered; 4/5 zombie

** Both recovered and eaten

We added a frailty for random plot effects (see above) to the fitted model to check whether and how inter-dependence of seed fates within plots affected the parameters for the post-harvesting fate model. Finally, primary and secondary cache distance (the processes C and F) were again analyzed using Cox regression, in which we treated cache findings as events and distance-to-source as failure time (time elapsed while walking from source to cache). Including non-retrieved seeds as cases censored at the search radius allowed us to account for the search bias. The further procedure was the same as for seed harvesting and cache recovery. Model fitting was done using R 1.5.0 (Ihaka and Gentleman 1996).

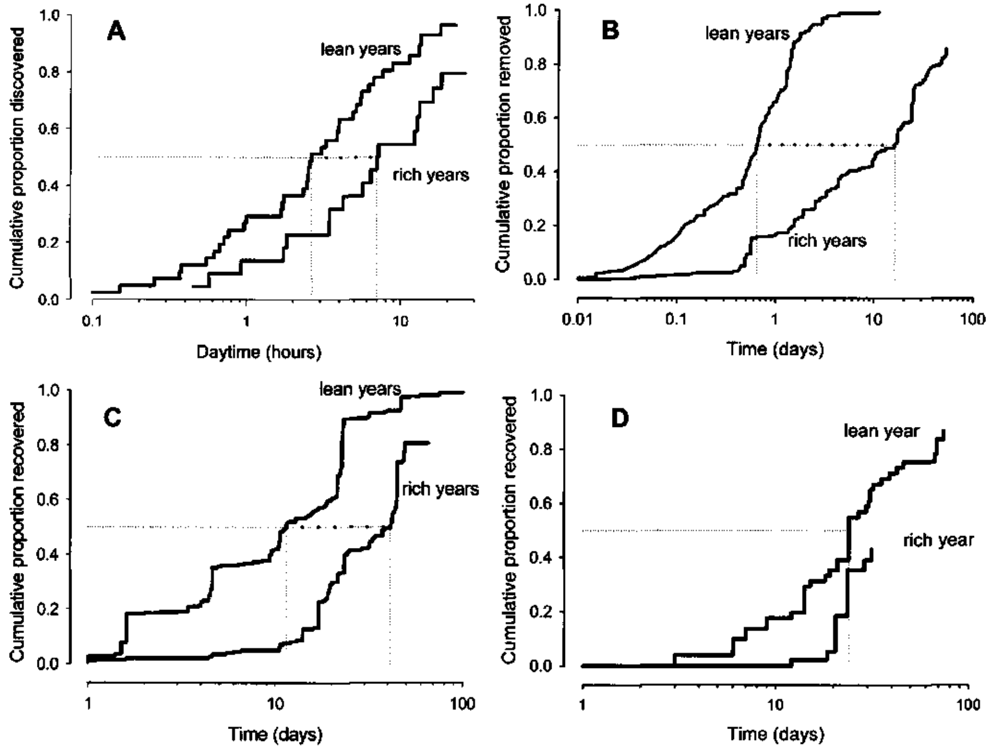


Figure 6.2 Effect of seed abundance on (**a**) discovery of seed plots by scatterhoarding rodents, (**b**) removal of seeds from plots, (**c**) recovery of seeds from primary caches and (**d**) recovery of seeds from secondary caches. Plots are inverse Kaplan Meier survival curves for lean years (upper lines) and rich years (lower lines). Dashed lines indicate median survival time. Note the difference in time scale between graphs.

Figure 6.1 (Opposite page) Seed fate pathways diagrams (*sensu* Price and Jenkins 1986) for rich years (upper part) and poor years (lower part). The boxes indicate seed fates, arrows indicate successional transitions of seeds between fates, starting at the plot. Numbers are numbers of seeds, percentages are adjusted proportions of the original sample (seeds at plot). The black boxes contain seeds that have successfully established seedlings. The shaded area contains all seeds that did certainly not establish. The fates 'not found' (seeds that we lost track of after removal / recovery) and 'censored' (seeds that were not removed / recovered within the monitoring period) represent incomplete ate records. Note that secondary and tertiary seed fates (survival of first and second order caches) were measured on sub-samples.

Figure 6.3 (opposite page, left column) Effect of seed mass and seed abundance on seed removal and scatterhoarding.

(**a**) Rate of seed removal as a function of seed mass ($\log_{10}$-scale) in lean years (filled dots, *n*=813 seeds) and rich years (open dots, *n*=1617 seeds). Dot size varies with sample size from 1 to 136 seeds. The rate of seed removal – calculated as the number of seeds removed divided by the total exposure time of all seeds – is the inverse of mean removal time. The minimum rate was set to 0.01 day^{-1}. Trend lines are weighted linear regression estimates of the removal rate for lean years (continuous line, $F_{1,25}$=11.5, *P*=0.002) and rich years (broken line, $F_{1,35}$=6.0, *P*=0.019).

(**b**) Total proportion of seeds removed as a function of seed mass ($\log_{10}$-scale). Symbols as in (a). Trend lines are logistic regression estimates of the removal probability, for lean years (continuous line, χ^2_1=43.1, *P*<0.001) and rich years (broken line, χ^2_1=59.8, *P*<0.001).

(**c**) Proportion of retrieved seeds in primary caches rather than eaten as a function of seed mass ($\log_{10}$-scale) in lean years (filled dots, *n*=597 seeds) and rich years (open dots, *n*=585 seeds). Dot size varies with sample size from 1 to 75 seeds. The trend line is the logistic regression estimate of the caching probability as a function of seed mass in lean years (continuous line, χ^2_1=7.5, *P*=0.006). There was no significant relationship with seed mass in rich years (*P*=0.083).

(**d**) Average cache distance as a function of seed mass ($\log_{10}$-scales) in lean years (filled dots, *n*=418 seeds) and rich years (open dots, *n*=414 seeds). Dot size varies with sample size from 1 to 52 seeds. Trend lines are linear regression estimates of cache distance for lean years (continuous line, $F_{1,416}$=70.9, *P*<0.001) and rich years (broken line, $F_{1,410}$=39.3, *P*<0.001).

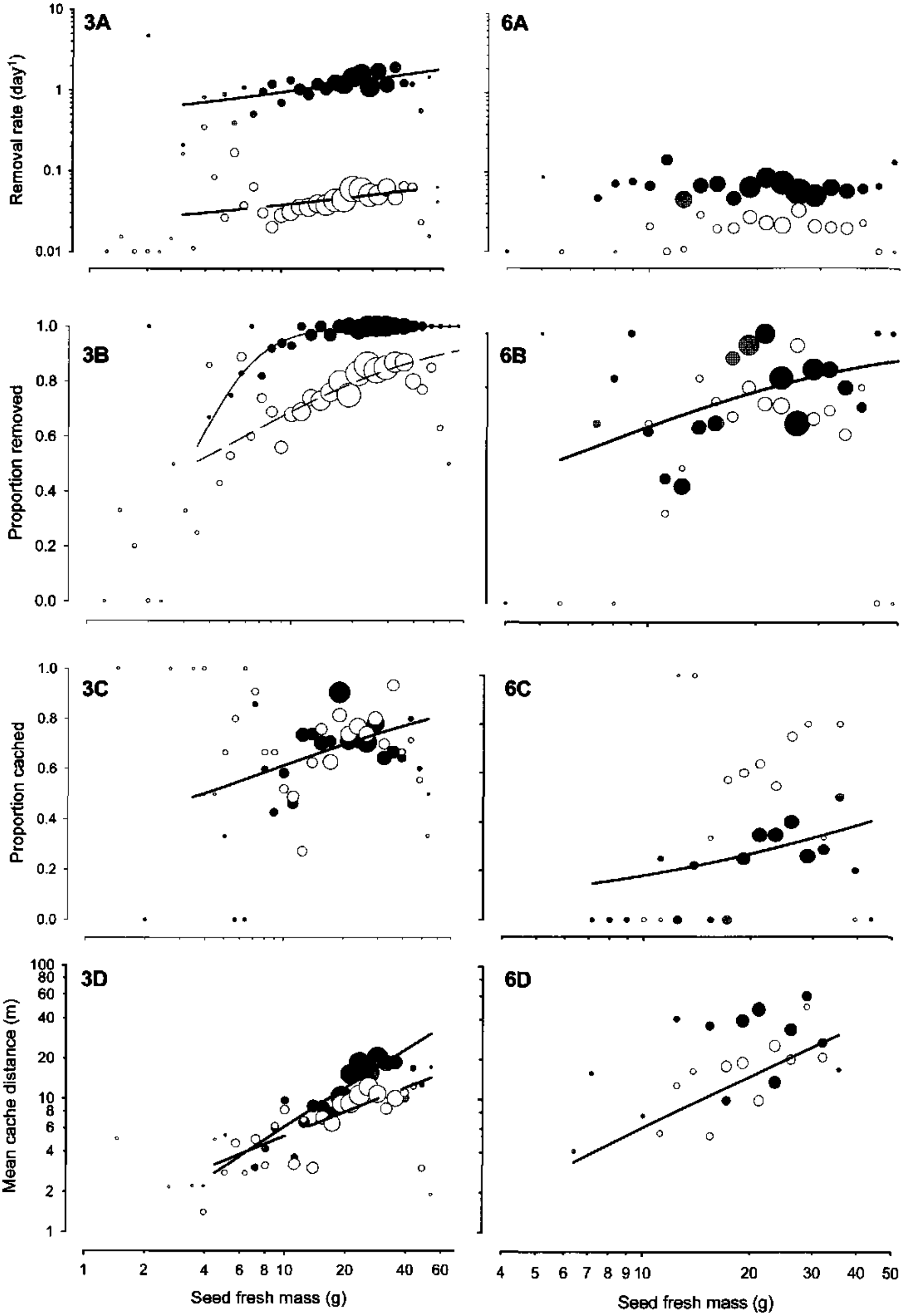
Figure 6.6 (opposite page, right column) Effect of seed mass and seed abundance on primary cache depletion and secondary caching.

(**a**) Rate of cache recovery (see FIGURE 6.3A) as a function of seed mass ($\log_{10}$-scale) in lean years (filled dots, *n*=498 seeds) and rich years (open dots, *n*=201 seeds). Dot size varies with sample size from 1 to 72 seeds. Weighted linear regressions of the removal rate on seed mass were not significant in either lean years (*P*=0.78) or rich years (*P*=0.403).

(**b**) Total proportion of seeds recovered from primary caches as a function of seed mass ($\log_{10}$-scale). Symbols as in FIGURE 6.3A. The trend lines is the logistic regression estimate of the removal probability in lean years (continuous line, χ^2_1=13.0, *P*<0.001). There was no significant relationship with seed mass in rich years (*P*=0.392).

(**c**) Proportion of retrieved seeds in secondary caches rather than eaten as a function of seed mass ($\log_{10}$-scale) in lean years (filled dots, *n*=204 seeds) and rich years (open dots, *n*=78 seeds). Dot size varies with sample size from 1 to 27 seeds. The trend line is the logistic regression estimates of the re-caching probability in lean years (χ^2_1=3.2, *P*=0.075). There was no significant relationship with seed mass in rich years (*P*=0.28).

(**d**) Average cache distance as a function of seed mass ($\log_{10}$-scales) in lean years (filled dots, *n*=58 seeds) and rich years (open dots, *n*=46 seeds). Dot size varies with sample size from 1 to 10 seeds. The trend line is the linear regression estimates of cache distance and rich years ($F_{1,44}$=6.4, *P*=0.015). There was no significant relationship with seed mass in poor years (*P*=0.21).


3A
6A
Removal rate (day^{-1})
10
1
0.1
0.01
3B
6B
Proportion removed
1.0
0.8
0.6
0.4
0.2
0.0
3C
6C
Proportion cached
1.0
0.8
0.6
0.4
0.2
0.0
3D
6D
Mean cache distance (m)
100
80
60
40
20
10
8
6
4
2
1
1
2
4
6
8
10
20
40
60
Seed fresh mass (g)
4
5
6
7
8
9
10
20
30
40
50
Seed fresh mass (g)

6.3 Results

The seed plots were discovered by seed-eating mammals very rapidly, indicating that seed removal was not detection-limited. In terms of daytime (time between 6:00 and 18:30), the median time till the first visit recorded on video was only 3:36 hours (n=59). Acouchies were more than ten times quicker in discovering the seeds than agoutis, peccaries and squirrels (pairwise log-rank tests: n=59, U_1>73, P<0.0001) and accounted for 94% of all first visits. Acouchies were always earlier than agoutis. Overall, discovery of plots by scatterhoarding rodents was quicker in poor years than in rich years (FIGURE 6.1A; Log-rank test: U_1=7.02, P=0.008). Video-recordings showed that subsequent harvesting was also primarily by scatterhoarding rodents, particularly acouchies (TABLE 6.3). In poor years, acouchies accounted for 82% of video-recorded harvesting, in rich years for even 100%. Intervals between acouchy removal events were mostly short and regular, indicating that early depletion of plots was mostly by a single individual. Seed harvesting by (collared) peccaries was concentrated at six plots visited by small herds. Agoutis were recorded harvesting seeds at as few as three plots (3%). Nocturnal activity at the plots was negligible.

The recorded fates of almost 3,000 *Carapa* seeds in rich and poor years are visualized in FIGURE 6.1A and 6.1B, respectively. Most seeds were harvested (*i.e.* selected by mammals for consumption or caching) within the observation times, but harvesting was more exhaustive in poor years (95%) than in rich years (78%). The speed of seed harvesting, however, differed dramatically between rich and poor years (FIGURE 6.2B; Logrank test: U_1=1777, P<0.001). While the median removal time was more than 16 days in the three rich years (mean hazard rate $h_0(t)$ = 0.05 day^{-1}), it was less than 16 *hours* in the two poor ones ($h_0(t)$ = 0.92 day^{-1}). The harvesting speed of seeds also increased with seed mass, especially in rich years (FIGURE 6.3A) and so did the proportion of seeds harvested (FIGURE 6.3B). There was a tendency of seeds greater than 40g fresh mass to be less rapidly and less likely harvested, but this was not significant. Previous studies of scatterhoarding at the same study site (Forget 1996) found that *Carapa* seed harvesting rates increased over the course of the season. In our study, harvesting rates did so in rich years but not in poor years. They converged towards the end of the fruiting season (FIGURE 6.4).

Years differed strikingly in pre-dispersal seed losses. In rich years, many seeds (24%) were infested and/or germinated while waiting to be harvested (FIGURE 6.1A), even though these processes occurred at fairly low rates. In poor years, in contrast, infestation and germination were zero. Germinated and infested seeds effectively lost prospects of establishment. Germinated seeds were still harvested and cached, but only after rodents pruned the protruding embryo, which changes these seeds into 'zombies' (CHAPTER 4). Germinated seeds that remained at the plots often got infested by insects and never established a seedling. Because germination and infestation played a role only in rich years, they enlarged the difference between poor and rich years. They also enlarged the difference between large and small seeds, because large seeds were harvested more rapidly and thus less likely affected. Remarkably, the germination rate of unharvested seeds never reached 50%, while *Carapa* normally germinates within 3-4 weeks after shedding. This suggests that non-dispersed seeds in our experiments suffered from desiccation, to which recalcitrant *Carapa* seeds are known to be sensitive (Connor *et al.* 1998; Ferraz-Kossmann and De Tarso Barbosa Sampaio 1996). Endosperm decay of

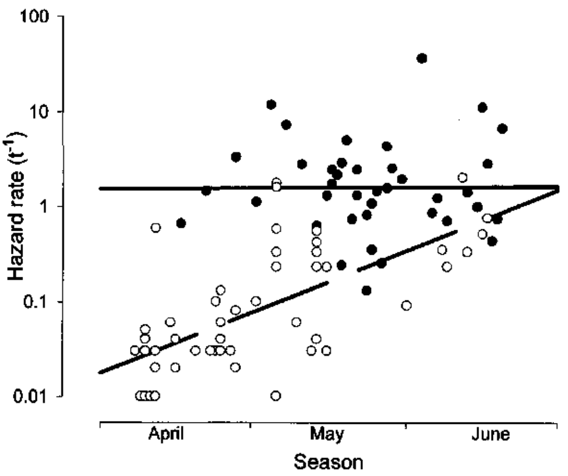


Figure 6.4 Effect of season and seed abundance on the speed of seed harvesting from cafeteria plots. Plotted is the hazard rate *h*(*t*) of seed harvesting throughout the fruiting season for rich years (open dots) and poor years (filled dots). Each dot represents a 25- or 49-seed cafeteria plot. The regression lines differ significantly in slope between poor (continuous line) and rich years (broken line) (General Factorial Model of log-transformed hazard rate: $F_{3,86}$=71.8, P<0.001, R^2=70%).

desiccated seeds is not visible from the outside, and was therefore not recorded by us. It seems fair to assume that *Carapa* seeds lost attractiveness to scatterhoarders as they laid exposed for a longer period.

To play apart the effects of seed mass and seed abundance from effects of covariates, we carried out an integrated Cox regression analysis of seed harvesting (TABLE 6.4). The baseline hazards show a clear effect of seed abundance, supporting HYPOTHESIS 1A: harvesting was more rapid in poor years and at the poorer site (FIGURE 6.5A). The slower depletion of 49-seed plots compared to 25-seed plots in rich years also indicates satiation (TABLE 6.4). The effect of seed mass was also significant, in agreement with HYPOTHESIS 1B, and was stronger in rich years than in poor, in agreement with HYPOTHESIS 1C (TABLE 6.4). To make sure that these results were not due to inter-dependence of seed fates within plots, we looked how the hazard ratios were affected by inclusion of a frailty for plots in the models. The hazard ratios increased rather than decreased (results not shown), indicating that the effects were not an artifact of deviant behavior by particular seed harvesting individuals.

Post-harvest seed fate

We relocated 55% of almost 2,500 seeds that were eventually harvested. Most of these were cached – all in single-seeded caches. The principal removal agents – acouchies – ate as few as 8-10% of the seeds they harvested (TABLE 6.3). The remaining seeds removed by these animals were found in single-seeded caches (52-75%), or not retrieved (38-18%). For reasons explained in the methods section and below, many of the latter seeds may in fact have been dispersed beyond our search area. In poor years, seed predation by mammals was greater (21%) than in rich years (6%), particularly due to peccaries that competed with acouchies for resources. In rich years, pre-dispersal germination and infestation severely reduced the probability of harvested seeds being scatterhoarded: few parasitised seeds (7%), moldered seeds (13%), and germinated seeds (14%) were found cached.

Overall, the proportion of harvested seeds that we found cached was greater in poor years (39%) than in rich (25%) (FIGURE 6.1). However, the proportion of seeds found eaten by mammals was also greater in poor years (21%) than in rich years (11%). The key is in the unknown fate non-retrieved seeds, many of which will in fact have been cached. Searching was more effective in poor years due to the stricter timing (immediately after the rapid depletion of plots) compared to rich years (after partial depletion of plots). *Rich years therefore had more non-retrieved seeds. The total percentage of seeds cached* may have been fairly similar between rich and poor years (approximately 45-50%), in spite of the differences in seed harvesting speed and pre-dispersal losses. Seeds found cached tended to be slightly heavier than seeds found eaten, on average 2g (*t*-test: $t_{1352}=3.86$, $P<0.001$) and discrimination against small seeds seemed stronger in rich years than in poor (FIGURE 6.3c). Non-retrieved (far-cached) seeds were in turn 1.4g heavier than seeds found cached (*t*-test corrected for unequal variances: $t_{2271}=5.28$, $P<0.001$).

Table 6.4 Effect of seed mass and seed abundance on the dynamics of *Carapa procera* seed harvesting. Cox regression models of **(a)** time-to-removal of seeds from experimental cafeteria plots, and **(b)** time-to-recovery from natural primary caches. Data shown are hazard ratios, showing the effect of one unit increase in the variable on the harvesting rate. In case of the binary covariates, the ratio is between two groups. Models were obtained by backward deletion of variables using BIC at K=2, and separate effects of seed mass and seed abundance from effects of experimental set-up and loss of seed quality in the study species. Rich and poor years were analyzed separately, and stratified by site because hazard functions were not proportional.

	(A) Seed removal rate		(B) Cache recovery rate	
	Lean years	Rich years	Lean year	Rich year
Main effects				
Seed fresh mass	1.20 $^{\text{N.S.}}$	1.58 ***	*n.s.*	2.11 $^{\text{N.S.}}$
Season	0.95 ***	1.17 ***	0.97 ***	1.02 *
Distance to source	n/a	n/a	0.84 $^{\text{N.S.}}$	0.75 $^{\text{N.S.}}$
Covariates [1]				
Plot size	n.s.	2.34 ***	n.s.	n.s.
Germination	n/a	n/a	n.s.	2.52 **
Parasitism	0.01 $^{\text{N.S.}}$	0.38 ***	n.s.	n.s.
Fungal attack	n/a	0.633 $^{\text{N.S.}}$	n/a	n.s.
Gnawing	0.153 $^{\text{N.S.}}$	0.289 $^{\text{N.S.}}$	n/a	n.s.
Test statistics				
Wald statistic	36.5 ***	241 ***	60.8 ***	40.8 ***
d.o.f.	4	6	2	4
n [2]	1198 (66)	1270 (365)	315 (3)	142 (55)

---

[1] Plot size was a fixed covariate with values 0 (49 seeds = reference) and 1 (25 seeds), the other variables were time-dependent covariates with values 0 (not affected = reference) and 1 (affected).

[2] Sample sizes are subdivided in uncensored and, between brackets, censored cases.

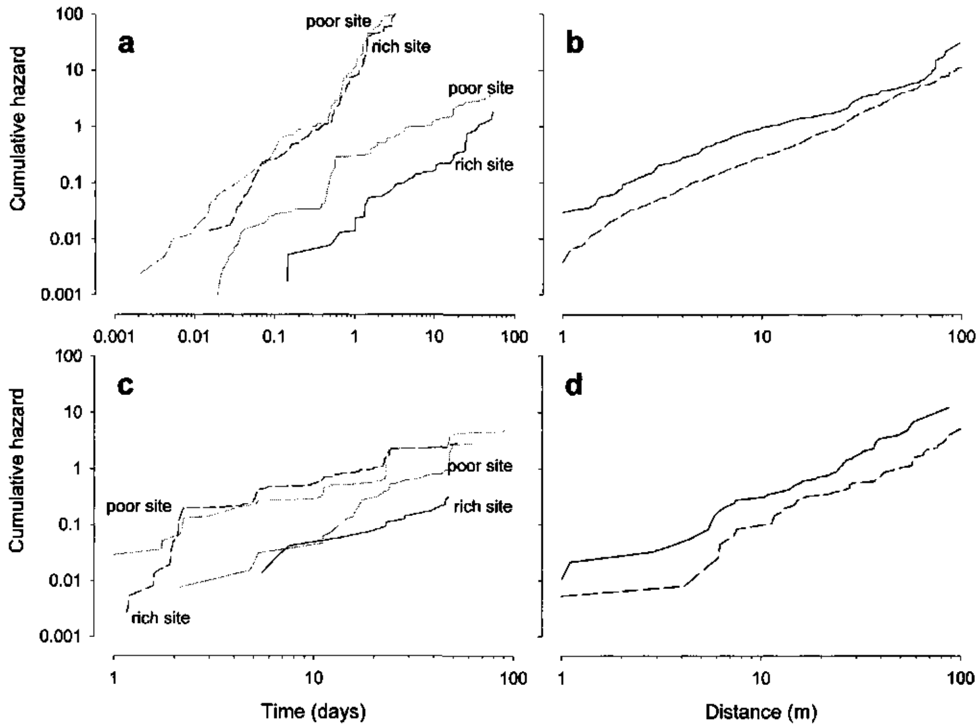


Figure 6.5 Effect of seed abundance on rates of seed handling by granivorous mammals. Baseline hazards for seed harvesting (**a**), primary cache distance (**b**), seed recovery from primary caches (**c**), and secondary cache distance (**d**), belonging to the Cox proportional hazard models in tables 6.4 and 6.6. Continuous lines indicate rich years, broken lines indicate poor years.

We fitted a logistic regression model of post-harvesting seed fate to again play apart the effects of seed mass and seed abundance from effects of covariates (TABLE 6.5). A clear positive effect of seed mass emerged, in agreement with HYPOTHESIS 2B. However, there was no significant effect of seed abundance, nor an interaction of abundance and mass, contrary to HYPOTHESES 2A AND 2C. Seeds were significantly less likely cached towards the end of the season in poor years but not in rich years (effect cancelled out by the interaction term). Other results were a greater likelihood of caching for seeds in small seed plots and seeds in the poor site. Inclusion of a frailty for plots in the models increased rather than decreased the odds ratios (results not shown), indicating that the effects were not due to inter-dependence of seed fates within plots.

Dispersal distance

The 922 primary seed caches that we found – 900 intact and 22 non-viable seeds – were at distances from 0.5m up to as far as 124m from the source. The median dispersal distance was greater in poor years than in rich years. Also, larger seeds were dispersed further, and this was stronger in poor years than in rich years (FIGURE 6.3D). Seeds were cached in different directions, which meant that further dispersal translated into a greater

Table 6.5 Effect of seed mass and seed abundance on the fate of *Carapa procera* seeds handled by seedeating mammals in French Guiana. Logistic regression models of the probability being (re-) cached for **(a)** seeds harvested from experimental cafeteria plots, and for **(b)** seeds recovered from natural primary caches. In each case, the left model uses only retrieved seeds, the model right assumes that non-retrieved seeds were also cached. Data shown are odds ratios, showing the effect of one unit increase in the variable on the probability of caching. Models were obtained by backward deletion of variables using BIC at K=2.

	(a) Caching probability		(b) Re-caching probability	
	Only findings	Incl. censors	Primary caches	All caches
intercept	3.71 *	1.71 $^{N.S.}$	0.04 *	0.05 *
Main effects				
seed abundance	0.18 ***	0.11 ***	0.22 $^{N.S.}$	0.13 *
seed fresh mass	1.86 ***	2.23 ***	3.17 **	3.51 **
season	0.93 ***	0.93 ***	0.98 $^{N.S.}$	0.96 ***
abundance x mass	n.s.	n.s.	n.s.	n.s.
abundance x season	1.09 ***	1.10 ***	1.06 **	1.06 ***
Covariates				
Plot size	3.60 ***	6.23 ***	n.s.	3.04 $^{N.S.}$
Site	1.27 $^{N.S.}$	2.35 ***	1.71 $^{N.S.}$	2.05 *
Exposure time	0.89 ***	0.91 ***	n.s.	n.s.
Parasitism	0.34 $^{N.S.}$	0.18 **	n.s.	n.s.
Germination	n.s.	n.s.	3.29 *	3.52 *
Fungal attack	n.s.	0.19 *	n/a	n/a
Stock time	n/a	n/a	0.97 $^{N.S.}$	n.s.

isolation of caches. The median neighbor distance, our measure for cache isolation, increased linearly with cache distance, and did so more strongly in poor years than in rich years, and more so at the Grand Plateau than at the Petit Plateau (General Factorial analysis, untransformed data: $F_{3,839}$=2294, P<0.001, R^2_{adj}=89%), indicating more efficient scattering under food scarcity. There was no additive effect of seed mass on cache isolation, indicating that density reduction was a side effect of dispersal (Jansen *et al.* 2002).

The fact that non-retrieved seeds were larger while cache distance increased with seed mass suggests that many non-retrieved seeds had been dispersed beyond our search radius than small seeds. It is likely that they were cached, as it makes no sense to carry seeds far to eat them. Indeed, consumption of seeds immediately after harvesting (i.e. within 5 days after the last sighting at the plot) tended to occur much closer to the source than caching: most consumed seeds (75%) were at or right next to the cafeteria plot. Moreover, among seeds found away from plots, consumed seeds were also much closer than cached seeds (Log rank test: U_1=26.3, P<0.001). Beyond 10m, as few as 5% of the 321 retrieved seeds were eaten, including seeds from rapidly recovered caches. Thus, our results likely underestimate the effect of seed mass on scatterhoarding and dispersal distance.

Table 6.6 Effect of seed mass and seed abundance on scatterhoarding. Cox regression models of distance-to-source for (**a**) primary caches and (**b**) secondary caches. Cache findings were treated as 'events' and cache distance was treated as 'time-to-event'. Non-retrieved seeds were censored at the search radius. Data shown are hazard ratios. Germination, parasitism and fungal attack were not significant, nor were interactions. Models were obtained by backward deletion of variables using BIC.

	(a) Primary cache distance		(b) Secondary cache distance
	Lean years	Rich years	Both years
Main effects			
Seed abundance	n/a	n/a	3.84 ***
Seed fresh mass	0.41 ***	0.48 ***	0.28 *
Season	n.s.	n.s.	1.02 *
Covariates			
Site	0.32 ***	n.s.	0.40 *
Plot size	n.s.	2.81 ***	n.s.
Test statistics			
Wald	183 ***	105 ***	41 ***
d.o.f.	2	2	4
n [1]	498 (344)	421 (161)	98 (247)

[1] Sample sizes are subdivided in uncensored and, between brackets, censored cases. Seeds that were re-cached in the primary cache were not treated as secondary caches.

We fitted a Cox model to analyze dispersal distance taking into account set-up, season and seed quality as well as seeds that were likely cached beyond the search radius. Here, we treated cache findings as events and distance-to-source as failure time, and censored non-recovered seeds at the search radius. Dispersal distance significantly increased with seed mass and was significantly larger in poor years, in agreement with HYPOTHESES 3B AND 3A, respectively (TABLE 6.6A). There was, however, no significant interaction, which disagrees with HYPOTHESIS 3C.

Survival of scatterhoarded seeds

We followed the fate of primary 616 caches of intact seeds in three years. Most were recovered by mammals within the (variable) observation period, but more so in the poor years (94%) than in the rich year (73%). Cache recovery was slower in the rich year than in the poor years (FIGURE 6.2C). The lifetime of primary caches, however, showed no relationship with seed mass (FIGURE 6.4A). If anything, the proportion of seeds recovered even increased with seed mass, particularly in poor years (FIGURE 6.4B), which is opposite to our predictions. Seeds in 'surviving' primary caches did not differ in mean seed mass from the original population in either the rich (one-sample *t*-test: $t_{1,53}$= 0.22; P=0.82) or the poor years ($t_{1,25}$= – 0.69; P=0.50), suggesting that 'survivors' were a random subset of the caches.

The effect of seed abundance on cache survival was also significant in the fitted Cox model (TABLE 6.4B), supporting HYPOTHESIS 4A. The baseline hazards (FIGURE 6.5B) show the same effect of seed abundance as those for seed harvesting (FIGURE 6.5A), with more rapid harvesting in poor years and at the poorer site (Grand Plateau). The hazard ratios further increased over the course of the season in lean years, while they decreased in rich years. Negative effects of seed mass and positive effects of cache distance on cache lifetime were not significant, and there was no interaction between seed abundance and seed mass, which disagrees with HYPOTHESES 4B AND 4C. Germination significantly enhanced cache recovery, indicating that sprouts were used as cues.Secondary dispersal

We retrieved 53% of 536 seeds recovered from primary caches. Many were in secondary caches rather than eaten. The proportion of retrieved seeds re-cached was greater in rich years (59%) than in poor years (28%) (FIGURE 6.4C), and increased with seed mass (FIGURE 6.4C). Seeds found re-cached tended to be slightly heavier than seeds found eaten, on average 1.6g (unequal variance *t*-test: $t_{253.5}$=2.06, P=0.041), and non-retrieved seeds were in turn heavier than cached seeds, again suggesting that many were cached at greater distances. The fitted logistic regression model (TABLE 6.5B) showed that the positive effect of seed mass on the probability of being re-cached was significant, confirming HYPOTHESIS 5B. However, there was no significant effect of seed abundance, nor an interaction of abundance and mass, which disagrees with HYPOTHESES 5A AND 5C. Moreover, as in post-removal caching, seeds were significantly less likely re-cached towards the end of the season in poor years but not in rich years. Finally, germinated seeds were more likely re-cached than non-germinated seeds, suggesting that rodents did not consider these 'zombie' seeds any less valuable than untreated seeds.

The 105 secondary seed caches – including 17 known zombies – were found at dispersal distances up to 114m from primary caches. Larger seeds were re-dispersed further, but this effect was significant only in rich years (FIGURE 6.4D). Secondary dispersal moved seeds significantly further away from seed plots (*t*-test: t_{103}=6.75, P<0.001), increasing the net dispersal distance by 13.5m on average. The furthest secondary cache that we found was as far as 160m from the original source. The fitted Cox model, taking into account censored cases, showed that secondary dispersal distance, just like primary dispersal distance, significantly increased with seed mass and was significantly larger in poor years (TABLE 6.6B), in agreement with HYPOTHESES 6B AND 6A, respectively. There was, however, no significant interaction between seed mass and seed abundance, which disagrees with HYPOTHESIS 6C.

We monitored the survival of 98 secondary caches – including 16 zombies – for variable lengths of time, in one poor year (1999) and one rich year (2000). The patterns were similar to those for primary seed caches (FIGURE 6.2D). Recorded depletion was greater in the poor year (80%) than in the rich year (40%). Cache recovery was more rapid in the poor year (median survival time 24 days) than in the rich (45 days) and the proportion of caches depleted after one month was also greater in the poor year (84%) than in the rich (30%). We retrieved 57% of 53 seeds recovered from secondary caches, some of which (40%) were in tertiary caches. The proportion of retrieved seeds eaten was greater in poor years (74%) than in poor years (21%). Seeds found re-cached were also heavier (25.1g, n=12) than seeds found eaten (21.0g, n=19; *t*-test: t_{29}=2.05, P=0.049). Inclusion of these caches did not alter the logistic model of re-caching (TABLE 6.6B), suggesting that they were not treated differently.

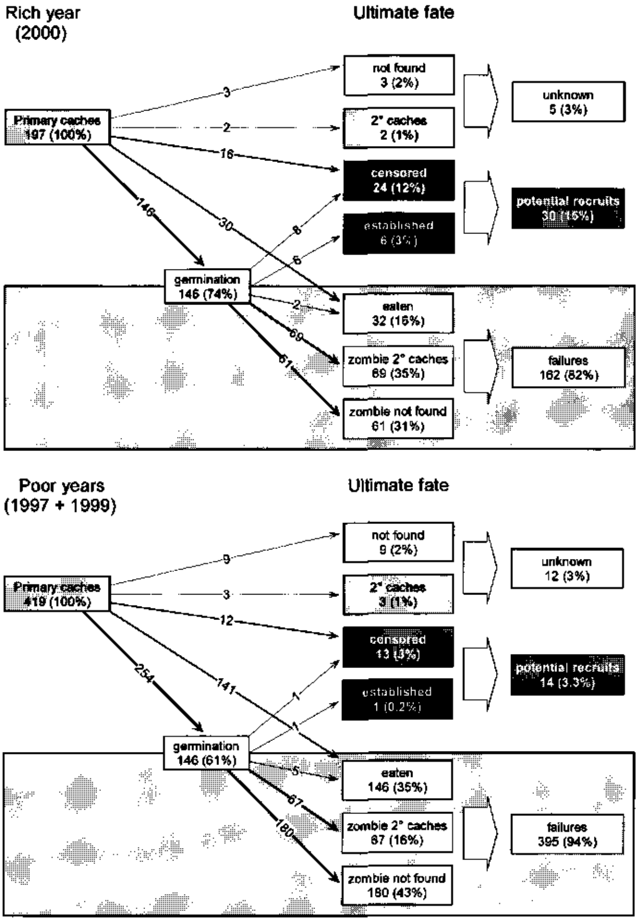


Figure 6.7 Seed fate pathways diagrams for primary caches of intact *Carapa* seeds, in rich years (**a**) and poor years (**b**), adjusted for 'zombies' to evaluate the number of successful seeds. Data are as in FIGURE 6.1, with the additional assumptions that (i) half of the recorded primary caches were in fact secondary caches with zombies, that (ii) 95% of recorded secondary caches and non-retrieved seeds were also zombies, and that (iii) these percentages hold for poor years as they do for rich. We did not change the pathways of consumed seeds, because it does not matter for recruitment whether seeds are consumed before or after germination. See FIGURE 6.1 for further explanation.

Seedling establishment

Since no seedlings established at the cafeteria plots, all recruitment came from intact seeds that germinated and established in caches. We recorded germination from only 18% of caches in the rich year (*n*=230 intact seeds) and no more than 3% in the poor years (*n*=468). We probably missed many germination events because our census schedule became coarser over time. Most observed germination events (71%, *n*=55) were interrupted by rodents that dug up germinating seeds and severed the germ, thus precluding further germination. We found most of these 'zombie' seeds re-cached, sometimes at the same spot. At the end of our observations, we had 6 established seedlings (0.7%) in the rich year and as few as 1 established seedling (0.1%) in the two

Table 6.7 Average seed mass for different seed fates, in the course of the scatterhoarding process. Given are average seed fresh masses (g), with sample sizes (between brackets). The category 'not retrieved' includes many seeds that were (re-)cached beyond our search radius.

	plot	1st caches	2nd caches	3rd caches
Rich years				
all seeds	21.5 (1644)	23.9 (201) †	23.2 (47) †	-
censored *	18.6 (366) ‡	24.0 (58)	23.0 (33)	-
harvested *	22.3 (1278)	23.8 (143)	23.7 (14)	-
eaten **	20.1 (172)	22.1 (32)	19.2 (3)	-
(re-)cached **	21.7 (423)	23.2 (47)	26.2 (7)	-
not retrieved **	23.3 (680)	25.4 (60)	22.7 (4)	-
established ***	-	27.4 (6)	-	-
Poor years				
all seeds	22.4 (1264)	23.1 (419) †	24.3 (51) †	23.5 (5) †
censored *	19.2 (65) ‡	21.8 (26)	25.9 (8)	22.8 (1)
harvested *	22.6 (1199)	23.2 (393)	24.0 (43)	23.7 (4)
eaten **	20.3 (271)	22.3 (146)	21.3 (16)	21.6 (2)
(re-)cached **	22.6 (499)	24.0 (58)	23.5 (5)	-
not retrieved **	24.1 (392)	23.7 (159)	26.1 (22)	24.8 (3)
established ***	-	28.4 (1)	-	-

* Subset of all seeds; ** subset of all harvested seeds; *** subset of all censored seeds; † (subset of) cached seeds in the previous column; ‡ Seeds that were not harvested from the cafeteria plots.

poor years, all from primary caches. The corresponding per-capita probability of establishment for seeds in primary caches was 13 times greater in rich years (3.0% of 197) than in poor (0.2% of 419) (G-test: G_{adj}=8.12; $P<0.005$), which is in line with HYPOTHESIS 7A.

For a fair comparison of recruitment success, however, we must also consider potential recruitment from seeds that were still cached intact. To find out whether censored caches contained viable seeds that could still produce seedlings, we dug up all remaining caches at the end of our study in 2000. Surprisingly, many more seeds were 'zombies' than only those that we had seen germinating and subsequently displaced. Censored primary caches contained 44% zombies (*n*=54), and censored higher order caches even 95% (*n*=40). Given their event histories, most of these seeds had germinated in primary caches – without us noticing – and be taken out by rodents and re-cached as zombies at the same spot. This made clear that our cache survival monitoring had not recorded all germination and zombie-treatment events. Rodents had apparently taken seeds out of caches and put them back again, without us noticing that the cache had actually been retrieved. If we assume that these observations also hold for poor years, we can redraw the seed fate diagrams for primary caches (FIGURE 6.7). Assuming that no secondary caches survive, the maximum per-capita probability of recruitment is 4½ times higher in rich years than in poor, still supporting HYPOTHESIS 7A.

TABLE 6.7 shows how discrimination against small seeds during the processes of harvesting and caching changed the average seed mass of seeds over time. The most important differences in size are between harvested and non-harvested seeds from the cafeteria plots, and between consumed seeds on the one hand and (re-)cached and non-retrieved seeds on the other. In other words, rodent feeding decisions based on seed seeing (smelling) or handling depend on seed size. The established seedlings were a non-random subset of the seeds that were originally laid out. They were much larger, which agrees with HYPOTHESIS 7B. Due to the small sample sizes, we cannot determine whether the difference in seed mass was greater in rich years than in poor. The stronger overall trend of disfavoring small seeds throughout the scatterhoarding process in rich years, however, supports HYPOTHESIS 7C. That the overall effect of seed mass was stronger in rich years is the more important because these years yielded most seedlings.

6.4 Discussion

Most published studies of seed dispersal by wild animals rely on assumptions about the identity of animals dispersing seeds (but see Hallwachs 1994; Jansen *et al.* 2002; Beck and Terborgh 2002). Video monitoring enabled us to identify which mammal species was responsible for the harvesting of each individual seed. We found that acouchies – rather than agoutis or other rodents – were the principal vector dispersing live *Carapa* seed away from the parent neighborhood, accounting for an estimated 90% of seed harvest. This rodent scatterhoarded at least two third of the harvested seeds into single-seeded caches. The majority remained within 25m from the source, but some seeds were dispersed further than 100m away, which is beyond the acouchy home range size postulated by Dubost (1988). Subsequent re-caching of recovered seeds could even further increase dispersal distance. The furthest seed that we found was eaten at 160m from its source. This is much further than previously documented for *Carapa* (Forget 1996) or any other seed species dispersed by scatterhoarding rodents. We think that scatterhoarding rodents pilfering each other's caches may transport seeds across several different, overlapping territories.

Scatterhoarding clearly increased the probability of seed survival and seedling establishment in *Carapa*. Even though the majority of cached seeds were recovered and consumed by rodents and other seedeaters, several seedlings established from caches. Non-dispersed *Carapa* seeds, in contrast, were never successful. None of 215 seeds germinating at the plots established a seedling. These results confirm conclusions from previous studies on large-seeded species. Newly established *Carapa procera* and *Licania alba* seedlings in understorey generally come from buried seeds (CHAPTER 8; unpublished data). Similar conclusions have been drawn for *Vouacapoua americana* (Forget 1990), *Hymenea courbaril* (Hallwachs 1986), *Bertholletia excelsa* (Peres and Baider 1997). Burial of seeds by rodents has been shown to promote germination and establishment in several rainforest tree species (Asquith *et al.* 1999; Smythe 1989; Sork 1987).

It was important for *Carapa* seeds that scatterhoarding took place rapidly. Long exposure on the forest floor increased parasitism and fungal attack, which made seeds unattractive for rodents to cache. Aging itself also seemed to negatively affect seed quality and reduce the interest of rodents, who seem to ignore old seeds if fresh seeds are available. Reduced odor, drying out (Ferraz-Kossmann and De Tarso Barbosa Sampaio 1996) and spoilage may result in lower attractiveness of old seeds in case of *Carapa*. Also, the longer seeds laid waiting to be harvested, the more likely was premature germination. Because rodents always pruned the embryo while handling germinated *Carapa* seeds, changing seeds into 'zombies' (CHAPTER 4), this effectively ruled out establishment. Manipulation of the germinability of seeds has also been observed in other scatterhoarding rodents (e.g., Steele *et al.* 2001). Finally, being handled by animals became more risky as time passed by; seeds were less likely (re-) cached as the end of the fruiting season approached, indicating that animals started to draw upon their reserves. A similar seasonal effect has been observed in *Tamias* chipmunks (Vander Wall 2002).

Given the locations of our plots, the seed removal patterns are representative only for adult trees in closed forest. Seedling establishment from non-scatterhoarded seeds, however, is definitely possible below *Carapa* trees standing in or along tree fall gaps (CHAPTER 8). Here, debris facilitates rooting of germinating seeds and light availability reduces the dependence of seedlings on seed reserves, compensating for the negative effects of high seed parasitism (Hammond and Brown 1998). These situations, however, are uncommon in natural forest.

The survival of caches was low, which is logical as rodents store seeds to postpone not abandon consumption. Whether acouchies also remember the locations of their caches, like Grey squirrels (Jacobs and Liman 1991), is not known. Our observations suggest that rodents used emerging sprouts as cues to find cached seeds, as was observed for agoutis by (Smythe 1978). Many germinated seeds were dug up, pruned and put back at the very same spot, which suggests that the rodents actively managed their caches to intervene in germination. None of the pruned seeds, which have a storage life of several months (CHAPTER 4), were seen dug up again.

In our study, only primary caches produced seedlings. The higher order caches mostly contained 'zombies' that would not germinate again. This suggests that the survival of primary caches is a good measure of establishment in *Carapa*, and that it is not essential to follow the fate of recovered seeds into secondary or even higher order caches. Measuring *Carapa* seed dispersal is strenuous because of long-distance caching, but measuring post-dispersal survival is much easier compared to species with slow germination or dormancy whose seeds can be recovered and re-cached several times before they germinate (e.g., Vander Wall and Joyner 1998; Vander Wall 2002; Xiao unpublished).

Although several rodents at our study site scatterhoard seeds, *Carapa* dispersal was primarily by a single one of them, the Red acouchy. If this pattern is general, *Carapa* is vulnerable for dispersal failure. Unlike agouti and other terrestrial rodents, Red acouchy in French Guiana inhabits only undisturbed forest areas (Dubost 1988), suggesting that *Carapa* will less effectively disperse in disturbed forest. However, *Carapa* is a widespread species that occurs in areas where acouchies are absent and other species – including agoutis – disperse the seeds. This suggests that the species is not strictly dependent on acouchies, and that other species take over dispersal where acouchies fail.

Mast seeding

We found enormous differences in seed fate between years of seed abundance (rich or 'mast' years) and years of seed scarcity (poor or 'non-mast' years), especially in the early phases (FIGURE 6.1). Scatterhoarding of *Carapa* seeds appeared better in poor years, with more rapid and more exhaustive seed harvesting and further dispersal. However, the proportion of seeds that finally got scatterhoarded was comparable between rich and poor years. A much better survival of seed caches in rich years subsequently outweighed the advantage of rapid harvesting in poor years. In other words, rich years yielded a comparable amount of caches per seed but significantly more seedlings per cache. The per capita probability of *Carapa* seeds establishing a seedling was at least 4½ times higher in rich years than in poor years. So, even though a putative masting species itself, *Carapa* benefits most from the years in which it produces large crops together with masting nut-bearers such as *Licania alba* and *Vouacapoua americana* that rely on the same dispersal agents. These findings also show that low seed removal rates are not necessarily indicative for poor dispersal or low recruitment.

These results support the predator satiation hypothesis for mast seeding (Salisbury 1942; Janzen 1971), even though our study did not include predation on developing seeds. Satiation was most apparent for seed-eating mammals, which caused less predation in rich years, both during harvest and after scatterhoarding. Predation by insects occurred *only* in rich years, which seems to argue against insect saturation. This apparent inverse contrast between rich and poor years, however, is probably an artifact of mammals overruling insects in poor years: rodents harvested and buried the seeds before insects could even get to them. That the insect population was indeed saturated with seeds to lay their eggs on is suggested by the low percentage of seeds parasitised even after several weeks of exposure. Insect saturation remains important because parasitism would not only affect the resources for future seedlings, but also reduced the probability of dispersal by rodents to almost zero.

Carapa seeds can escape rodent predation by germinating and transferring seed reserves into seedlings, which are unpalatable food to rodents. Keeping this idea in mind, we propose that rich years yielded more seedlings for two reasons. Caches were more abundant, and the rodents were unable to timely manage the numerous seeds that germinated simultaneously. And, the perceived value of individual seeds was lower, and the rodents were less motivated to intervene in germination. Clearly, both are satiation effects. The lower recovery rates of caches in rich years provide greater windows of opportunity for cached seeds to germinate and establish.

We found that seeds were harvested less rapidly and buried less far in rich years than in poor. This agrees with the basic optimal foraging principle of animals investing less in food items of a lower perceived value (Stapanian and Smith 1978). However, seeds from 49-seed plots were dispersed further than those from 25-seed plots, which supports the hypothesis that large seed crops stimulates scatterhoarders to cache seeds further in order to achieve the same low density of caches (Stapanian and Smith 1978). In other words, dispersal distance increases with crop size, but is reduced by ambient seed abundance.

Table 6.8 Population-level studies of scatterhoarding and mast-seeding in nut-bearing plants. A 12-year study by Gurnel (1993) was not included because it did not provide removal data at the species level. Indicated is how scatterhoarding animals treated seeds in years of seed abundance compared to years of seed scarcity. The contrast between rich and poor years in the study by Hoshizaki and Hulme (2002) was arbitrary, which may explain why this study is deviant.

tree species	disperser	site	seed mass (g)	sample size	No. of years (poor-rich)	removal rate
Beilschmiedia bancroftii	rat	Australia	51	120	1-1	slower
Carapa procera	acouchy	French Guiana	21	2899	2-3	slower
Aesculus turbinate	woodmouse	Japan	19	300	1-2	variable
Quercus robur	woodmouse	Brittany	3.5	<2000	1-1	slower
Pinus lambertiana	chipmunk	Nevada, US	0.29	1440	1-2	equal
Pinus jeffreyi	chipmunk	Nevada, US	0.15	1440	1-2	equal
Pinus ponderosa	chipmunk	Nevada, US	0.06	1440	1-2	equal

Table 6.9 Intra-specific seed fate studies of scatterhoarding and seed mass in nut-bearing plants. Studies marked with * used peanut fruits and coconut pieces as artificial nuts. Indicated is how scatterhoarding animals treated large seeds in comparison to small ones.

tree species	disperser	site	seed mass (g) (contrast)	sample size	removal rate
Arachis hypogaea *	Squirrel	Canada	0.8 / 1.5	120	
Quercus serrata	rats	China	0.8 / 1.5	800	equal
Quercus oleoides	Agouti	Costa Rica	2.3 - 5	>1104	
Quercus robur	Jays	Netherlands	0.5 - 7.5	700	
Astrocaryum mexicanum	mouse	Belize	5.8 / 14.3	320	faster
Cocos nucifera *	Agouti	Costa Rica	0.5 - 30	?	
Carapa procera	Acouchy	French Guiana	2 - 56	2899	faster
Beilschmiedia bancroftii	rats	Australia	28 - 85	147	

Table 6.8 Continued.

scatterhoarding			cache survival				
% removed	% cached	cache distance	recovery rate	% recovered	% recached	seedlings (ratio)	source
equal	equal	shorter	slower	equal	?	?	Theimer 2001
equal	equal	shorter	slower	lower	lower	4.5-13	This study
equal	higher	?	?	equal	higher	2	Hoshizaki & Hulme 2002
equal	?	?	?	?	?	?	Crawley & Long 1995
equal	equal	equal	slower	lower	lower	14.6	Vander Wall 2002 /2003
equal	lower	equal	slower	lower	lower	4.1	Vander Wall 2002 /2003
equal	equal	longer	slower	lower	lower	2.2	Vander Wall 2002 /2003

Table 6.9 Continued.

scatterhoarding			cache survival			
% removed	% cached	cache distance	recovery rate	% recovered	seedling recruitment	Source
	higher	further				Hurly & Robertson 1987
equal	equal	further	lower	lower	higher	Xiao, unpublished
	higher	further				Hallwachs 1994
higher						Bossema 1979
higher	equal	closer	higher	higher	lower	Brewer 2001
	higher	further				Hallwachs 1994
higher	higher	further	equal	higher	higher	this study
variable	variable	variable				Theimer 2003

Seed fate studies that compare scatterhoarding between years of contrasting seed abundance are few, and some include few years and small samples. Yet, the patterns of seed fate that emerged are remarkably similar (TABLE 6.8). Several studies found that seed harvesting was slower under seed abundance. However, none of the studies found a difference between years in the proportion of seeds that was ultimately harvested, while the proportion of seeds cached also tended to be similar. The effect of seed abundance of cache distance was variable between studies.

Thus, seed abundance affected the rate of seed removal but not the extent of scatterhoarding. Moreover, all studies found slower cache recovery and most greater survival of cached seeds in rich years. The overall pattern is that seeds in rich years are more likely to establish seedlings.

The only other tropical study by Theimer (2001) matches our results best. Theimer found no difference in the percentage of seeds harvested by White-tailed rats (*Uromys cudimaculatus*), although harvesting was much slower in the mast year than the non-mast year. Although Theimer saw no seeds germinating let alone establishing, cache lifetimes were longer in the mast-year (49 versus 8 days). Vander Wall's (2002) conclusions – the value of cached seeds in rich years is lower, pilfering rates are lower, seeds are handled by rodents less often, resulting in higher seed survival compared to poor years – apply to acouchies and *Carapa* in Guianan rainforest as well as they applied to chipmunks and *Pinus* in Nevada's dry woodland.

Seed mass

Several papers have now studied how seed size influenced the effectiveness of scatterhoarding rodents, mostly by inter-specific comparison (e.g., Stapanian and Smith 1984; Clarkson *et al.* 1986; Vander Wall 1995; 2003; Forget *et al.* 1998). TABLE 6.9 lists studies that varied seed size within species like we did. Within-species comparisons are especially suitable for the evaluation of the seed size selection hypothesis, because they control for other factors than seed mass, such as nutrient composition, digestibility and defense (Hurly and Robertson 1987). The drawback, however, is the more limited range in seed size of within-species studies. Because our study species is highly variable in seed size, we were still able to cover a 20-fold within-species range of seed fresh mass.

We found that seed dispersal and survival were positively related to seed mass in *all* stages of the scatterhoarding process, confirming most predictions (TABLE 6.1) which were in turn based on optimal foraging theory (Stephens and Krebs 1986) and optimal cache spacing models (Stapanian and Smith 1978). Scatterhoarding rodents clearly discriminated between seeds based on seed size. Large seeds were harvested more rapidly and scatterhoarded more often than small seeds, and they were cached further away, which translated into greater isolation from sibling caches. Seed mass did not directly affect cache survival, but because more distant, isolated caches have longer lifetimes (Stapanian and Smith 1984; Clarkson *et al.* 1986), large seeds ultimately had a greater probability of surviving and establishing a seedling. All seedlings recorded in this study came from large seeds. These findings support the seed size selection hypothesis (Smith and Reichman 1984), which explains the comparatively large seed mass in tree species dispersed by scatterhoarding animals as an evolutionary response to selection by these animals favoring larger, more nutritious seeds above smaller, less nutritious ones.

Discrimination against small seeds during seed harvest and scatterhoarding has been found in most intra-specific seed fate studies (TABLE 6.9), but not all. Theimer (2003), for example, found a tendency of discrimination against both the smallest and the largest seeds, while some other studies did not find selectivity during harvest at all (see paragraph below for a possible explanation). All studies found a greater likelihood of caching and a greater dispersal distance for larger seeds, except for Brewer and Webb (2001), who found the inverse. A possible explanation is that the large seeds in Brewer's study were heavy (14.3g) and big (61mm length) compared to Spiny pocket mouse dimensions (55g). They may have been beyond the point at which seed manipulation becomes increasingly difficult and expensive, pushing down the net benefit of scatterhoarding (CHAPTER 7). In our study the largest seeds were also doing worse than the intermediate ones. The studies are too few and too variable to distinguish common trends in the probability of seedling establishment. The study by Xiao (unpublished) matches our results best.

Seed mass and seed abundance

No published studies of seed mass and scatterhoarding consider how disperser selectivity is affected by seed scarcity (but see Vander Wall 2002 and 2003 combined). It is, however, likely that selectivity is temporally variable, and especially affected by the degree of seed scarcity perceived by foragers. Jansen *et al.* (2002) argued that rodents cannot afford being selective under strong seed scarcity, because they then need all seeds to build up sufficient reserves. If indeed scatterhoarders become selective once they have secured sufficient supplies for surviving the forthcoming dry season or winter, differences in the background seed availability may explain why some studies found discrimination against small seeds during seed harvest (Stapanian and Smith 1984; Clarkson *et al.* 1986; Hallwachs 1994; Vander Wall 1995; Brewer and Webb 2001; Vander Wall 2003) whereas others did not (Theimer 2003; Xiao, unpublished). These findings underline that the circumstances under which seed fate experiments are carried out greatly influence the outcome, which must certainly be taken into account when comparing experiments.

There are limits to the reproductive effort any individual can make due to nutritional and physical constraints. Smith and Fretwell (1974) hypothesised that these limits imply that seed size and seed number are traded-off, and that plant species must find an optimal balance between producing big seeds and producing many. Our findings suggest that nut-bearing trees can maximise scatterhoarding and minimise seed predation by producing large crops simultaneously with other nut-bearing trees in the population. At the same time, they must produce pretty big seeds to maximise the chance of scatterhoarding rather than instant consumption, and this is even more the case under seed abundance, when competition for dispersers is fierce. Mast seeding, the production of large synchronous crops of large seeds in alternation with several small crops, seems a perfect solution. Rather than trading off seed size and seed number within crops, mast-seeding trees trade-off resources between consecutive crops, displaying large and large-seeded crops in some years at the cost of crops in other years.

How mast seeding in nut-bearing species may relate to seed dispersal and seed predation by granivorous animals is shown schematically in FIGURE 6.8. The diagram which is an adaptation of the more general model presented by (Sork 1993). It differs from Sork's model in that it acknowledges the role of seed size and seed abundance to

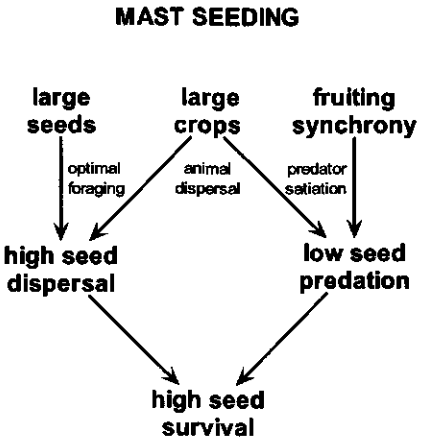


Figure 6.8 A model for the effects of seed mass and mast seeding on scatterhoarding and its effectiveness as dispersal mode. See SECTION 6.5 for explanation.

encourage dispersal. Moreover, it relates mast seeding only to the two alternative functions – predation and dispersal – of the community of seed-eating animals, and not to pollination effectiveness requiring massive and synchronous flowering or habitat conditions requiring large seeds. The underlying hypotheses indicated in the diagram are optimal foraging theory (Stephens and Krebs 1986) and optimal cache spacing theory (Clarkson *et al.* 1986; Stapanian and Smith 1978), the predator satiation hypothesis (Janzen 1974), and the animal dispersal hypothesis (Kelly 1994).

Conclusions

Our results supported most of the hypotheses on seed mass and seed abundance (TABLE 6.1), indicating that the seed production strategy of scatterhoarder-dispersed trees can be explained by optimal foraging theory (Stephens and Krebs 1986) and optimal cache spacing models (Clarkson *et al.* 1986; Stapanian and Smith 1978). The effectiveness of dispersal by scatterhoarding animals was governed by the seed value perceived by the animals, which was based both on seed nutritional content and ambient seed abundance. Larger, more nutritious seeds of *Carapa* had a higher probability of establishing a seedling than smaller ones, and *Carapa* seeds produced in years of seed abundance were more likely to establish a seedling than seeds produced in years of seed scarcity. Large seeds shed in rich years did best.

6.5 Acknowledgements

We thank to Martijn Bartholomeus, Marion Diemel, Jelmer Elzinga, Sander Koenraadt, Rick Middelbosch, and Anne Rutten for great fieldwork effort. We thank Pierre-Michel Forget for introducing us to the subject and for stimulating discussions, Frank Sterck and Jan den Ouden for commenting the manuscript, and Pierre Charles-Dominique for permission to work at the Nouragues Biological Station. This study was funded by the Netherlands Foundation for the Advancement of Tropical Research with grant W80-407 (Jansen).

7. Stabilising selection on seed size by a seed-dispersing rodent

A classic trade-off in plant evolutionary ecology is that between seed vigour and dispersability: seed and seedling vigour select for ever-larger seeds, while dispersal effectiveness selects for ever-smaller ones (Howe and Vande Kerckhove 1981; Smith and Fretwell 1984; Hedge *et al.* 1991; Kelly 1995). Recent studies, however, suggest that scatterhoarding animals provide better dispersal to larger seeds than to smaller ones (Hallwachs 1994; Forget *et al.* 1998; Jansen *et al.* 2002; Vander Wall 2002). It has been hypothesised that scatterhoarding animals have driven the evolution of large-seediness characteristic for nut-bearing plant species (Smith and Reichman 1984; Vander Wall 2001). Here we show that seed dispersal by scatterhoarding Red Acouchies in French Guianan rainforest favours intermediate-sized seeds rather than ever-smaller or ever-larger seeds. Video surveillance of seed harvesting from cafeteria experiments and tracking of dispersed seeds showed that intermediate-sized seeds were more rapidly removed, more likely cached, and further dispersed than smaller or larger seeds. We propose that scatterhoarding animals cause stabilising selection on seed size in the plant species they disperse.

7.1 Introduction

Seed mass varies among plant species by as much as ten orders of magnitude (Harper *et al.* 1970). Many of the largest-seeded plant species are dispersed by scatterhoarding animals such as rodents and corvid birds, which store numerous seeds in spatially scattered soil surface caches. A proportion of the cached seeds are eventually recovered and consumed, but the remaining ones are often in microsites than enhance germination and establishment (Vander Wall 1990). Recent intra-specific studies, controlling for variation in traits other than seed mass, have found that scatterhoarding rates and dispersal distance increase with seed mass (Hallwachs 1994; Jansen *et al.* 2002; but see Brewer 2001). These findings are opposite to the established idea that dispersal effectiveness decreases as seeds get larger, mainly based on wind-dispersed and frugivore-dispersed species (Jordano 1995; Howe and Westley 1996), but are consistent with optimal foraging theory (MacArthur and Pianka 1966) and optimal cache spacing theory (Stapanian and Smith 1978). Greater food value makes larger seeds more attractive to seedeaters and leads to greater investment in caching.

Clearly, however, even dispersal by scatterhoarding animals cannot increase with seed mass infinitely: there are limits to the size and mass of seeds that any scatterhoarding animal can carry given its own mouth width and body mass. The Double Coconut (*Lodoicea maldavica*, Palmae), for example, has a huge food value, but no

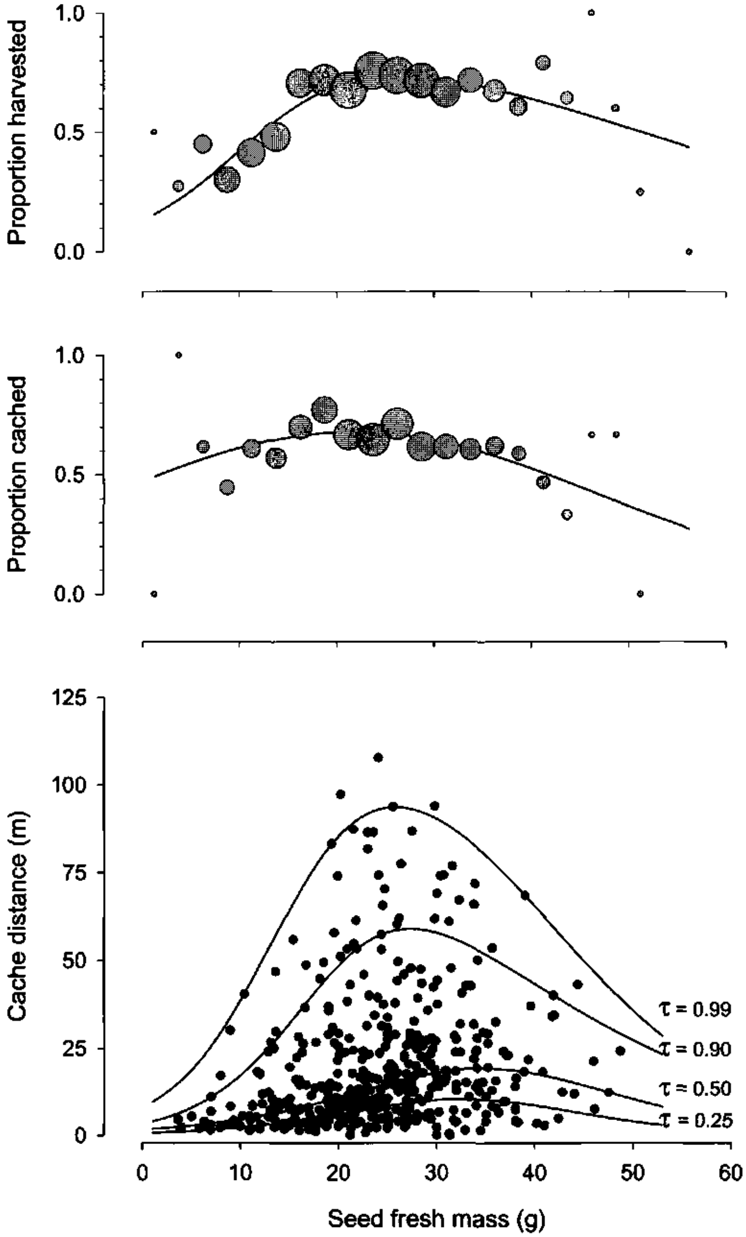


Figure 7.1 Seed size-dependent dispersal by acouchies. Effect of seed fresh mass on the proportion of seeds harvested by acouchies (**a**), the proportion of seeds that was subsequently retrieved in caches (**b**), and seed dispersal distance (**c**). Dot area (**a,c**) corresponds with the sample size of 5g-seed mass categories. Lines are best non-linear regressions for the binary data (**a,c**), and best non-linear quantile regressions for dispersal distance at four quantiles.

existing rodent can effectively disperse the 20-kg seed. For each animal species, a threshold seed size must exist beyond which manipulation becomes increasingly difficult and expensive. We therefore hypothesised that an optimum seed size exists for seed dispersal by a given scatterhoarding animal species, and selection pressure by these animals should be stabilising towards this optimum, rather than directional to ever-smaller or -larger seeds.

7.2 Results

We studied seed dispersal by the Red Acouchy (*Myoprocta exilis*), a scatterhoarding rodent of *ca.* 1kg body mass that is common in the Guianas and Amazon, at the Nouragues rainforest reserve in French Guiana, 100km south of Cayenne (4°02'N, 52°42'W). We established cafeteria plots of individually numbered, thread-marked seeds. We used seeds from a single tree species with highly variable seed size, so we could widely vary seed mass within plots while controlling for seed chemical composition (Hurly and Robertson 1987). We then monitored harvesting of individual seeds by acouchies with video surveillance cameras. Acouchies accounted for 94% of all recorded seed removal (757 seeds). We found that the seeds most often removed by acouchies were the intermediate-sized (optimum at 27g; FIGURE 7.1A). The speed of seed harvesting showed an identical pattern (not shown). Subsequently, we did area surveys to retrieve harvested seeds, using threadmarks protruding from the soil to locate buried seeds. We found that the harvested seeds most likely to be retrieved in caches were again the intermediate-sized (optimum at 22g; FIGURE 7.1B). Small and large seeds were most likely eaten or not retrieved. Lastly, we found that intermediate-sized seeds had the furthest dispersal (FIGURE 7.1C). The best quantile regression models for $\tau=0.25$, $\tau=0.50$, $\tau=0.90$ and $\tau=0.99$ had optima between 26 and 35g seed mass.

Overall, acouchy selectivity narrowed the distribution of seed mass in the experimental seed cohort (FIGURE 7.2). Selection against smaller seeds was strong and significant during all stages of scatterhoarding, indicating that scatterhoarders preferentially harvest seeds of greater food value and invest more in caching such seeds (Stapanian and Smith 1978). Large seeds were selected against in the caching phase but not during harvesting. This is consistent with the idea that the animals prefer larger, more nutritious seeds, but that seed handling and thus transport becomes increasingly difficult above a certain seed size. Selection against large seeds is the more important for plants because the largest seeds are also the most expensive to produce (Smith and Fretwell 1984).

7.3 Discussion

Losses during plant life history are greatest in the seed-to-seedling phase (Harper 1977). In large-seeded plants, whose seeds are sensitive to predation by non-mutualist seedeaters and are likely killed below the parent plant if not removed by a disperser, scatterhoarding can greatly enhance seed survival. The probability of seeds escaping predation increases as scatterhoarding animals cache seeds at greater distances, which translates linearly into lower seed densities (Jansen *et al.* 2002) and thus lower expected

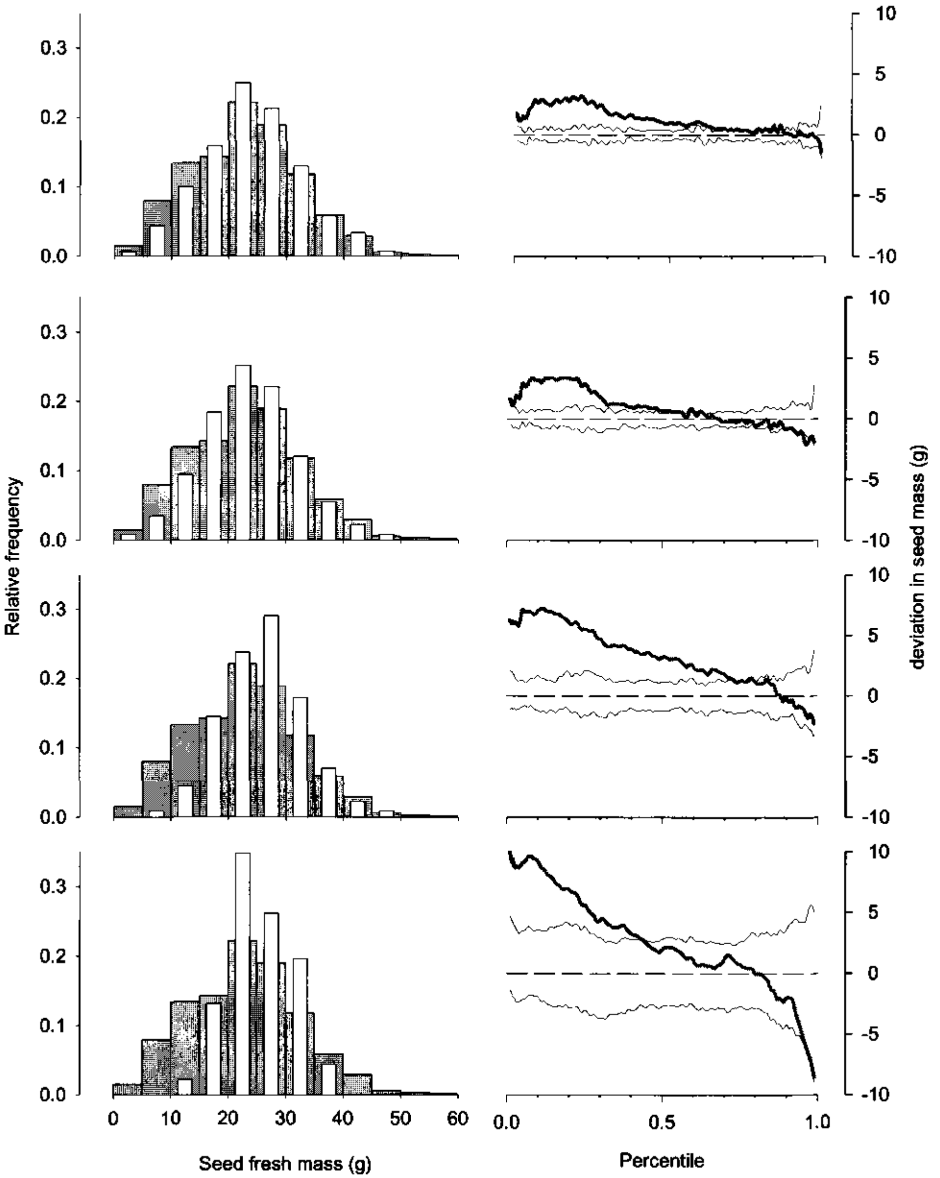


Figure 7.2 Narrowing of the seed size distribution in response to acouchy preferences. The shaded area in figures **a-d** shows the initial distribution of seed mass in the experiment per 5g-category, the white bars show the relative frequencies of mass for seeds harvested by acouchies (**a**), seeds cached by acouchies (**b**), the 50% subset of seeds with greatest dispersal distances (**c**), and the 10% subset of seeds with greatest dispersal distances (**d**). Right panel graphs (**e-h**) compare the distribution to randomisation test results standardised around the original percentile values. The dotted lines, enclosing 90% of the observed values among 1000 random samples at each individual percentile, are conservative one-sided test values at $\alpha<0.05$. Positive departures at the left end of the panel and negative departure at the right side indicate narrowing of the frequency distribution.

density-dependent mortality (Stapanian and Smith 1978). Our study shows that acouchies give the most favourable treatment to intermediate-sized seeds, rather than ever-smaller or ever-larger seeds as previously believed, resulting in a fitness advantage for intermediate-sized seeds. Because seed mass is a variable and heritable trait (Majonnier 1998) selectivity of scatterhoarding seed dispersers likely causes stabilising selection on seed size in their food plants.

7.4 Acknowledgements

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Appendix: Methods

Cafeteria experiments

The data presented in this paper come from 25 cafeteria plots, established during the fruiting seasons (April-June) of 1997-2000, each containing a grid of 25 or 49 seeds of *Carapa procera* (Meliaceae). This lower canopy tree, common in the Guianas and the Amazon, shows exceptional variation in seed mass between and within individuals, largely due to variation in the degree of fertilisation of the 20-ovule fruits. We used this variation to create experimental seed batches that ranged in fresh mass as widely as possible: from 6 to 44g on average per plot, with 1 and 57g as extreme values. Our study animals are the principal dispersers of *Carapa* at the study site (Forget 1996, Jansen *et al.* 2002). Seeds were individually numbered and thread-marked with 1m fluorescent fishing line and 8cm of pink fluorescent flagging tape. We used a battery-powered surveillance camera (Philips VCM 6250/00T) and time-lapse video recorder (Panasonic AG-1070 DC) to monitor harvesting of individual seeds without disturbing the animals. We recorded whether and when seeds were removed by acouchies during *c.* 600 total daytime hours of potential activity (24 ± 18 hours cafeteria^{-1}). Subsequently, we retrieved dispersed seeds by searching for thread-marks. Even when seeds are cached, these remain visible protruding from the soil. We surveyed at least a 25m-radius area around plots, and did non-exhaustive searching beyond that radius. We recorded whether and how far from the source seeds were cached.

Data analysis and testing

Data were analysed by comparing the fit of a hierarchical set of logistic models with upper bound *M* (Huisman *et al.* 1993) and a linear relationship. The most complex model was a 4-parameter asymmetric response curve,

$$y = M \cdot \frac{e^{a+bx}}{1+e^{a+bx}} \cdot \frac{e^{c+dx}}{1+e^{c+dx}}$$

with opposite signs for *b* and *d* (asymmetric response). Reduced models were obtained by setting d=-b (Gaussian response curve), d=0 (increase to a maximum <M), c=0 and d=0 (increase to maximum M), and all parameters to 0 except a (no response). Under stabilising selection, models with an optimum (the first two) should give a better fit than any other models. Models were fitted to binary data through maximum likelihood estimation (Hemerik *et al.* 2002) using the nlm procedure in R 1.5.0 (Ihaka and Gentleman 1996), with M=1. The Akaike Information Criterion (AIC; Akaike 1974) was used to identify the best model. The relationship between dispersal distance and seed size was analysed with non-linear quantile regression (Koenker and Park 1984), an iterative least squares technique for the exploration of heteroscedastic errors. We fitted the five hierarchical models to the 10th, 25th, 50th, 75th, 90th and 99th quantiles, using the nlrq procedure in R with M=125, the maximum dispersal distance observed for *Carapa* seeds (Jansen *et al.* 2002). The fitted regression quantiles describe the distance range within which a certain proportion of cached seeds was found. The upper quantiles approximate the maximum dispersal distance, and indicate limiting factors (Scharf *et al.* 1998; Cade *et al.* 1999). The criterion for identifying the best model was a minimum value of

$$\frac{SSQ(m)}{n-2m}$$

given *n* observations and *m* parameters (Efron and Tibshirani 1993).

Whether acouchy selectivity throughout the scatterhoarding process significantly narrowed the seed size distribution was evaluated by comparing the observed seed mass at each of 99 percentiles to the distribution of seed mass at these percentiles among 1000 random samples, drawn from the original size distribution. One-sided test values at α=0.05 were obtained by calculating the 90% envelope at each percentile. The test values are highly conservative because the set of most extreme values to which we compare our sample can come from different random samples at every percentile. In other words, we set off all-round performance against the highest performance at each part of the distribution.

8. Predator escape, gap colonisation and the recruitment pattern of three rodent-dispersed rainforest tree species

8.1 Introduction

Most seed plants in tropical rainforest invest enormous amounts of resources in structures enhancing seed dispersal. Why seed dispersal is apparently so important is a question still intriguing many researchers Wang and Smith (2002). The best-established idea is seeds must move away from their parent and siblings to avoid distance- and density-dependent mortality; the so-called 'escape hypothesis' or 'compensatory mortality hypothesis' (Connell 1971; Janzen 1970). Seeds in clumps, for example, can have a greater rate and/or probability of attack by herbivores than isolated seeds (Clark and Clark 1984; Hammond and Brown 1998; Hammond *et al.* 1999; Howe 1989; Stapanian and Smith 1984). Also, seedlings in clumps and near adults can be more likely infested by pathogens (Augspurger 1983a, 1993b; Augspurger and Kelly 1984). A second well-established explanation, which we shall call the 'gap colonisation hypothesis', is the requirement of gaps for seedling recruitment, because light is the major factor limiting growth and survival in many tropical rainforest plant species (Hammond and Brown 1998; Schupp *et al.* 1989). Even seedlings of species that are capable of surviving under low light conditions can be regarded as 'waiting' for canopy gaps to be created. Gaps are unpredictably distributed in space and time, and dispersal increases the probability of seeds hitting (present or near-future) gaps, because it scatters seeds over a larger surface (Augspurger 1983a).

Both the escape hypothesis and the gap colonisation hypothesis have been confirmed by several experimental field studies, which compare contrasts selected for the particular purpose of testing with maximum control for other factors (Clark and Clark 1984; Hammond and Brown 1998). Determining the importance of these mechanisms in real forest, however, requires the study of seedling recruitment in natural situations. Here, gap presence is negatively correlated to adult proximity, simply because gaps host fewer adult trees than non-gaps by definition. Also, the expected number of gap locations increases with distance-to-adult because the area around an adult tree increases exponentially with its radius, and, thus, so will the per capita probability of seeds encountering a gap of their own (Augspurger 1983a). Few studies have attempted to quantify spatial seedling recruitment distributions (Ribbens *et al.* 1994) and even fewer have considered light availability and adult proximity simultaneously (e.g., Augspurger 1983a). Weighing the importance of light availability and isolation, Hammond and Brown (1998) have hypothesised that gap presence is more important for regeneration than adult proximity, and those positive light effects counterbalance negative distance or density effects. The underlying idea is that higher photosynthesis makes plants in high light conditions less dependent on seed reserves and enables them to cope with attack by herbivores and diseases (but see Hammond *et al.* 1999).

Table 8.1 Characteristics of the study tree species. Seed samples were collected below parent trees in Nouragues in April 1996 (adapted from Jansen and Forget 2001).

	Species		
Properties	***Licania***	***Carapa***	***Vouacapoua***
Seed production			
Regularity	Irregular, synchronous	Annual	Irregular, synchronous
Period	March-May	April-June	April-May
Seed output	400 (max 1200)	500 (max 2250)	600 (max 1600)
Seed nutritional value			
n	25	63	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
Seed 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 analyses were done in duplo on a mixture of three uninfected seeds.

We studied the spatial pattern of natural seedling recruitment in three large-seeded canopy tree species in a French Guianan rainforest. The species have in common their dispersal exclusively by acouchies and agoutis, but differ in the extent of seed dispersal (Jansen and Forget 2001). If adults and gaps have a strong effect on recruitment in these species, the survival of seeds and seedlings should show a significantly positive relationship with gap proximity and adult distance. Moreover, the range of seed dispersal should visibly reduce the contribution of adult-dependent mortality. We compared the distribution of young and old seedlings with random distributions and seed shadows and tested three hypotheses: (1) Seedling recruitment is negatively related to the proximity of reproductive conspecifics (*i.e.* the escape hypothesis). The relationship affects species with poorer dispersal more strongly. (2) Seedling recruitment is positively related to the proximity of canopy gaps (*i.e.* the gap colonisation hypothesis). (3) Light availability is more important for seedling recruitment than the proximity of reproductive conspecifics.

8.2 Methods

Site and species

Data were collected in the Nouragues reserve, an undisturbed lowland rainforest site in French Guiana, 100km south of Cayenne, at 4°02' N and 52°42' W, and 100-150m above sea level. Annual precipitation averages 2900mm, with peaks in December-January and

April-July. Bongers *et al.* (2001) give an extensive description of the site. Our sampling site was at the so-called 'petit plateau', a relatively flat and homogenous part of the area. Previous studies have produced a detailed knowledge of the spatial distribution of canopy gaps and trees >10cm dbh in this area (Van der Meer and Bongers 1996, unpublished data).

The study species were three nut-bearing canopy trees common in the Nouragues area: *Carapa procera* (Meliaceae), *Licania alba* (Chrysobalanaceae) and *Vouacapoua americana* (Caesalpiniaceae). Species characteristics are given in TABLE 8.1. *Carapa* and *Vouacapoua* seedlings are known to perform better in treefall gaps (Forget *et al.* 1999). All species are dispersed by the Red acouchy (*Myoprocta acouchy*, Erxleben 1777) and the Red-rumped agouti (*Dasyprocta leporina*, L. 1758). These scatterhoarding rodents, which measure 33-39cm and 49-64cm length, respectively, and 1.0-1.5kg and 3.0-5.9kg (Emmons and Feer 1990), store seeds, their main food, by burying them in shallow caches in the topsoil, one seed per cache. Acouchies and agoutis produce a seed distribution that is remarkably over-dispersed and predictable compared to seed distributions from other dispersal modes, and is also well-documented (Forget 1990; Jansen and Forget 2001; Jansen *et al.* 2002; P.A. Jansen, unpublished data). The tree species differ in the range of dispersal and their vulnerability to predator attack. Nutritional value, mechanical protection against granivorous insects, time-to-germination, rate of seed removal, and dispersal distance are all lowest in *Vouacapoua* and highest in *Licania* (Jansen and Forget 2001).

Spatial distributions

We measured the spatial distribution of two age classes of seedlings with respect to reproductive adult trees and treefall gaps in the surrounding area. Thus, we treated adult trees as the centres of zones with low expected recruitment under HYPOTHESIS 1, and treefall gaps as the foci of seedling recruitment under HYPOTHESIS 2. We then tested for segregation and aggregation by comparing distance distributions with the seed shadow (*i.e.* the range of seed dispersal) and the random distribution. Under HYPOTHESIS 1, we expected that the distance-to-adult be as follows: older seedlings > young seedlings > seed shadow, and older seedlings > random distribution. Under HYPOTHESIS 2, we expected the distance-to-gap be as follows: older seedlings < young seedlings < random distribution.

Seed distributions (seed shadows) were obtained from existing studies of seed scatterhoarding in Nouragues that mapped positions of seeds after dispersal from experimental feeding plots (Forget 1990; Jansen *et al.* 2002; CHAPTER 6). We used the distance-to-source of primary caches, and censored all seeds that were removed but not found cached at the radius of our search area. Thus, we assumed that rodents only travel beyond that distance to cache seeds, not to eat them. Our experience from the field is that consumption of seeds immediately upon harvest tends to be in situ, and rarely >10m away from the source (CHAPTER 6). A second assumption is that subsequent management and exploitation of caches will only thin the seed shadow, not alter the distribution. Thus, we ignore net expansion of the seed shadow as a result of re-caching of viable seeds (Vander Wall 2003; Vander Wall and Joyner 1998). For *Carapa*, we know that this is safe, because recruitment comes from primary caches (CHAPTER 6), but for a slow-germinating species as *Licania*, we know that re-caching will likely further expand the seed shadow.

Licania and *Carapa* seedlings smaller than 1m were surveyed in a 200x200m (4ha) area in August 1999, *Vouacapoua* seedlings were inventoried in a 250x20 (0.5ha) area in November 1992. Seedlings were categorised by age, which we estimated by size, shoot number, leaf number and weariness, and the presence and condition of below-ground seed remains. In *Licania*, young seedlings included the cohorts from fruiting years 1996 and 1998, old seedlings the cohorts 1995 and earlier. In *Carapa*, young seedlings included the cohorts from 1997-1999, old seedlings the cohorts 1996 and earlier. In *Vouacapoua*, young seedlings grouped individuals from the 1992 cohort, old seedlings the earlier cohorts. In *Vouacapoua*, 66% of all seedlings were located in one patch that covered only 0.5% of the sampling area, and which was located far away from any parent tree or gap. We doubted whether this concentration was natural, and decided to exclude these individuals from further analyses.

Adult trees were mapped in a ~400x400m (15.4ha) area enclosing the seedling plots in 1993 and 1999. Which individuals were reproductive was determined by checking for fruits and fruit remains in tree crowns and below trees (during the fruiting season of 2000, a mast year, for *Vouacapoua* and *Licania*, and several times between 1995 and 2000 for *Carapa*). Reproduction occurred from 17cm dhb with probability $(1 + e^{8.4 - 0.34 \times \mathrm{DBH}})^{-1}$ in *Carapa* (logistic regression: *n*=122, Wald=28.0, *P*<0.001), from 26cm with probability $(1 + e^{3.8 - 0.12 \times \mathrm{DBH}})^{-1}$ in *Vouacapoua* (*n*=76, Wald=19.1, *P*<0.001), and from 16cm with probability $(1 + e^{3.0 - 0.13 \times \mathrm{DBH}})^{-1}$ in *Licania* (*n*=146, Wald=31.7, *P*<0.001). However, the seed output of small reproductive individuals was often so modest that their role as seed source and focus of predators and pests was doubtful. Therefore, we included all individuals >35cm dbh in each species, supplemented with all *Licania* >26cm dbh that we actually saw producing seed, and all *Carapa* >30cm with a yearly seed output >100 seeds.

The occurrence and size of treefall gaps was recorded in the same 16ha area between 1990 and 1997 (Van der Meer and Bongers 1996). We included only the gaps whose surface *sensu* Brokaw (1982) exceeded 3.5m². This is the area without leaf layers between sky and soil surface. Gap area was then measured as the polygon surface between the stem bases of all tree crowns bordering the canopy gap (Runkle 1981). Gap mapping was incomplete along the north-eastern side of the seedling plot, but this zone had no additional large canopy gaps close to the central 4ha.

The relative frequency of seedlings near adult trees standing along treefall gaps is of particular interest for our study. Under HYPOTHESIS 3, negative effects of adult proximity and seed and seedling density in these situations should be counteracted by light availability, resulting in high recruitment from seeds that were never removed from below adult trees and from seeds cached in the immediate vicinity. Our seedling sampling area, however, included no *Carapa* seed sources along treefall gaps. Therefore, we additionally counted seedlings below three such *Carapa* trees elsewhere in the 16ha area, and compared the numbers with similar-sized individuals in the 4ha.

Analyses

Spatial clumping of adult trees and of seedlings was analysed using Ripley's *K*-function (Ripley 1978): $K(t) = \lambda^{-1} \cdot E(d)$. Here, λ is the density of points and $E(d)$ is the number of neighbours within distance *d* from each point. We calculated $K(d)$ for 100 distances *d*, and transformed it to $L(d) = \sqrt{K(d)/\pi} - d$. This formula has an expectation of 0 under complete spatial randomness, and is thus easier to interpret. We obtained 95% and 99% confidence envelopes by calculating $L(d)$ for each of 1,000 random patterns of n points, and then determined the 0.5%, 2.5%, 97.5% and 99.5% quantile of $L(d)$ for the same 100 values of d. Since random patterns include the same edge effects as the original data, we did not apply further edge corrections.

We calculated the distance to the nearest conspecific seed source for all seedlings as well as for 10,000 random points within the sampling area. Similarly, we calculated the distance-to-gap of seedlings and random points as the distance to the nearest gap edge (*sensu* Runkle 1981) of each gap age category. Seedlings and random points located within gaps were given negative distances. We first analysed nearest-neighbour distances using a non-parametric approach resembling Hamill and Wright's (1986) technique. We calculated Kaplan-Meier distribution curves to show the frequency of individuals beyond a given nearest-neighbour distance. We tested for differences between curves using the log-rank statistic

$$U = \sum_{i=1}^{k} w_i (D_i - E_i)$$

in which D_i is the number of individuals found at distance i from the source, E_i is the expected number of individuals at distance i (calculated from the number of individuals beyond distance i-1 and at each distance interval in the sample), and w_i is a weighing factor. For our tests of HYPOTHESIS 1 (survival near adults is disproportionally lower), we used the Breslow (or generalised Wilcoxon) statistic. Here, w_i weighs the differences $D_i - E_i$ by the number of individuals beyond distance i. Hence, the Breslow test weighs findings near adult trees more heavily than findings at greater distances. For HYPOTHESIS 2 (survival away from gaps is disproportionally lower), we used the Mantel-Cox Log-rank statistic, in which $w_i = 1$, emphasising the tail of the distribution, *i.e.* differences in frequency away from gaps.

Subsequently, we used multiple logistic regression to analyse seedling occurrence as a function of distance to seed sources, different categories of treefall gap, and their interaction, as in Frost and Rydin (2000). We used the 10,000 random points mentioned above as zero values, and increased the distance-to-gap to set the minimum value to zero (seedlings in gaps have negative distances).

Mapping and calculation of distances to adults and gaps were done in ARCINFO. Ripley's K functions were calculated using the S+SPATIALSTATS 1.5 module in S-PLUS 2000 (MathSoft 1999). Other statistical analyses were done in SPSS 10.0.5 (SPSS 1999).

8.3 Results

Spatial distributions of adult trees in the 16ha and of seedlings against the background of seed sources and gaps in the sample plots are shown in FIGURE 8.1A-C and FIGURE 8.1D-F, respectively. The seed sources in the 16ha area were randomly distributed, with only some weak clumping in *Carapa* at scales <100m (FIGURE 8.2). Hence, the distribution of adult trees in our study area was sufficiently random to not bother about cumulative effects of adult proximity, and use the distance to the single nearest seed source as estimate of

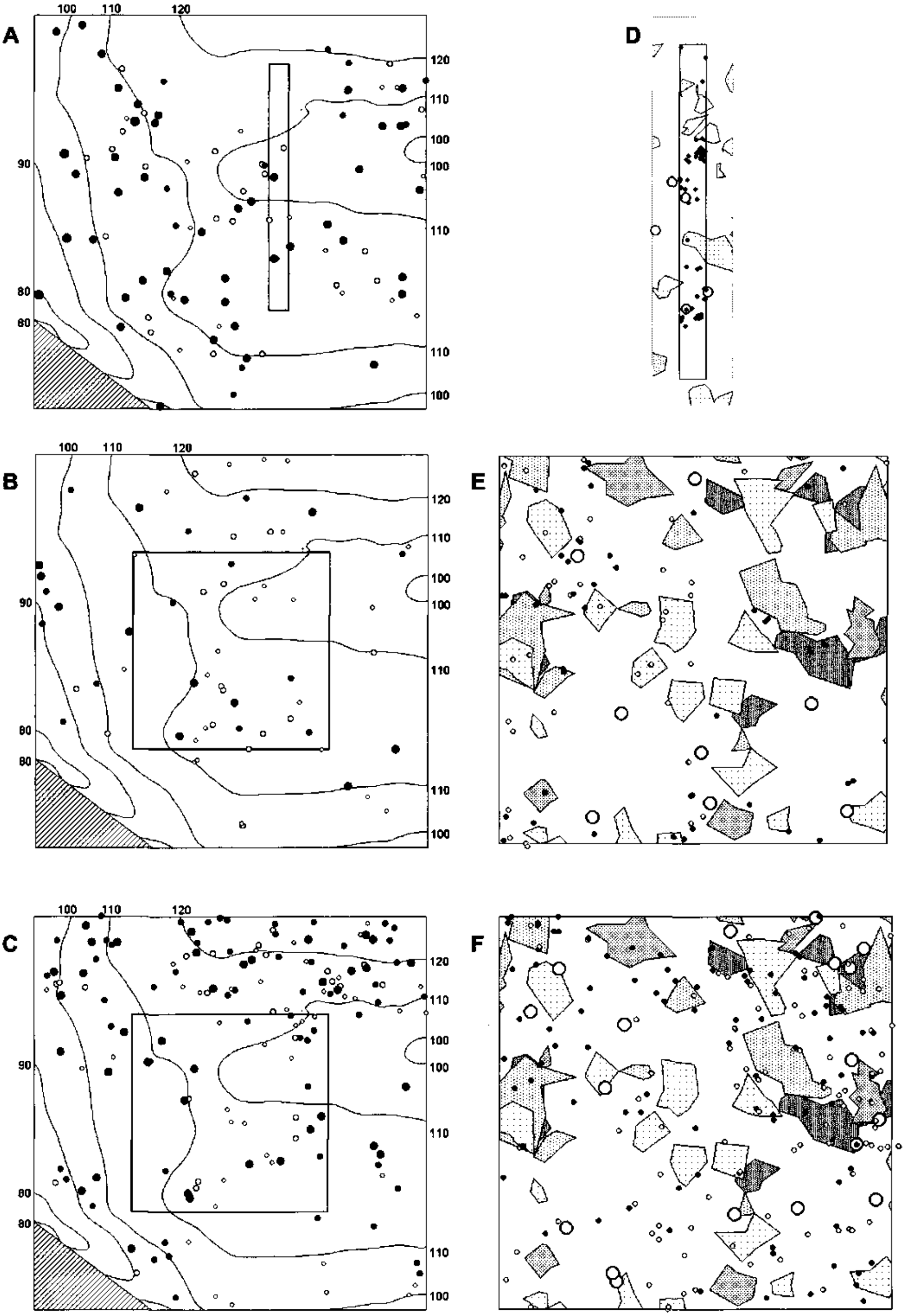
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Figure 8.1 (Opposite page) Spatial distribution of seed sources and seedlings of three rodent-dispersed tree species at Nouragues, French Guiana. **(a-c)** Maps of individuals >10cm dbh in a 400x400m (16ha) area. Dot size varies with tree dbh. Filled dots were classified as reproductive adults, open dots represent non-reproductive trees. Spatial distribution of seedlings in three rodent-dispersed tree species. **(d-f)** Maps of seedlings in the 200x200m (4ha) core area in August 1999 (*Carapa procera* and *Licania alba*), and in a 25x200m (0.5ha) subset in August 1992 (*Vouacapoua americana*). Filled dots represent young individuals, open dots represent older individuals <100cm tall (see text for definition of age categories). Large open dots are reproductive conspecifics. Polygons represent canopy gaps *sensu* Runkle (1985) categorised by age: dating from 1996-1997 (dark), 1993-1995, 1990-1992, and before 1989 (light). The white area represents closed forest.

adult proximity. The clumping of seedlings differed between species with the extent of seed dispersal. Young seedlings were strongly clumped at scale 10-40m in the poor-dispersed *Vouacapoua* (FIGURE 8.3A), weakly clumped at scale ~35m in *Carapa* (FIGURE 8.3B), and randomly distributed in the well-dispersed *Licania* (FIGURE 8.3C).

The Kaplan Meier distributions of seedling's distance-to-the-nearest adult as well as the seed shadows and the random distributions are shown in FIGURE 8.4. The differences between the distributions become smaller as dispersal increases going from *Vouacapoua* (Breslow test: U_3=729, P<0.001), to *Carapa* (U_3=681, P<0.001) and *Licania* (U_3=211, P<0.001). Under HYPOTHESIS 1, we expected that the distribution would shift to the right going from seed shadow to young seedlings to old seedlings, and that this shift would be strongest in the species with the poorest dispersal. The results showed this pattern, with the greatest shift in *Vouacapoua* and no shift at all in *Licania*. The seed shadow of *Licania* was even beyond the random distribution indicating that this species' dispersed seeds potentially covered the entire available area. This implies that dispersal is more extensive than necessary under the given density of adult trees. In *Vouacapoua*, the poorest disperser, young seedlings were located further from the nearest adult than expected from the seed shadow (Pair-wise Breslow log-rank test: U=15.84, P<0.001), older seedlings were located further away from adults than younger seedlings, although not significantly (U=2.12, P=0.14). Moreover, the distribution of older seedlings approached randomness (U=1.39, P=0.24). However, the seed shadow and seedling distributions were not significantly different in the better dispersers *Carapa* and *Licania*. Under HYPOTHESIS 1, we also expect the distribution of seedlings be more to the right than the random distribution (*cf.* Hamill and Wright 1986), especially at short distance-to-adult. None of the species, however, shows this pattern. We conclude that distance-dependent mortality is reflected only in the spatial pattern of seedlings in *Vouacapoua*. The spatial pattern of *Carapa* and *Licania* seedlings with respect to adults is random.

Under HYPOTHESIS 2, we expected that low survival under low light conditions would produce a low frequency of seedlings at large distances from canopy gaps relative to the availability of space. The Kaplan Meier distributions of distance-to-the-nearest treefall gap (FIGURE 8.4D-F) should move to the left going from random to young seedlings to old seedlings due to disproportionate thinning of the tail of the distribution. None of the species, however, showed the predicted pattern. Old seedlings were closer to treefall gaps than young ones, although not significantly, in *Vouacapoua* (Mantel-Cox Log-rank test: U_2=2.03, P=0.15), and *Carapa* (U_2=0.67, P=0.41) but not in *Licania* (U_2=1.80, P=0.18). None of distributions of old seedlings differed from the random distribution.

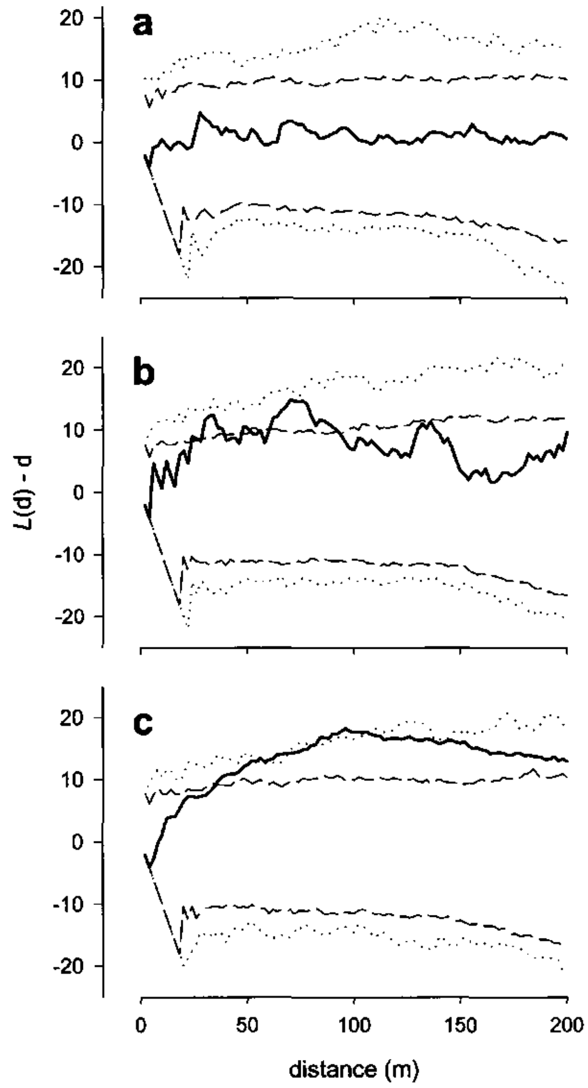

Figure 8.2 Second-order neighbour analyses of the spatial distribution of reproductive trees in *Vouacapoua* (**a**), *Carapa* (**b**), and *Licania* (**c**). The function *L*(*d*) is a transformation of Ripley's *K*, with expectation 0 under complete randomness (see method section). Broken and dotted lines indicate 95% and 99% confidence envelopes, respectively. Positive departures of *L*(*d*) indicate aggregation, negative departures indicate segregation of individuals at the scale of distance *d*.

Distance to gap and distance to adult may interact. Particularly adult trees standing along treefall gaps should have higher seedling recruitment in their immediate vicinity than adult trees standing in closed forest, if light availability indeed overrules density-dependent mortality (HYPOTHESIS 3). Moreover, it makes sense that seedlings be clustered around gaps of a particular age class rather than gaps in general: young seedlings might be associated with recent gaps, and older seedlings with older gaps. Therefore, we did

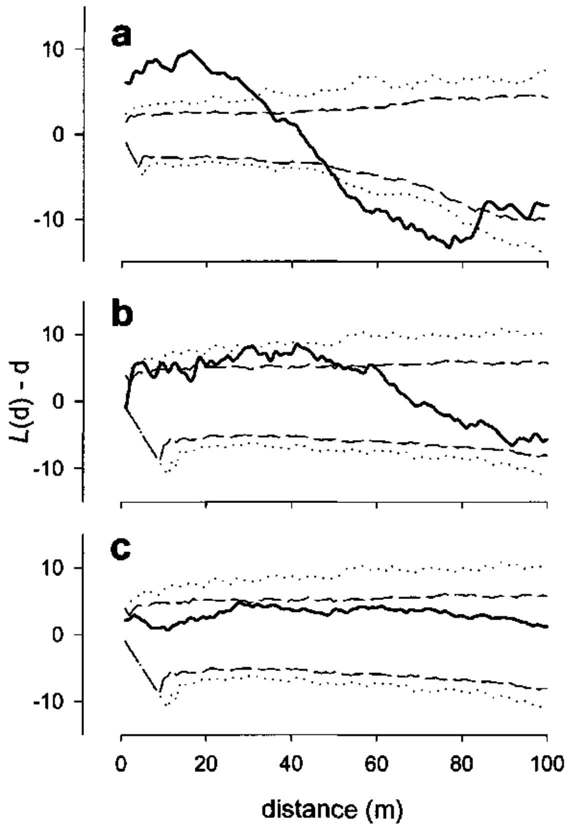

Figure 8.3 Second-order analyses of the spatial distribution of seedlings <1m height in *Vouacapoua* (**a**), *Carapa* (**b**), and *Licania* (**c**). See FIGURE 8.2 for explanation.

logistic regression analyses of seedling occurrence as a function of distance to adults and distance to different age classes of gaps (TABLE 8.2). Young seedlings were associated with adults in *Vouacapoua*, to a lesser extent in *Carapa*, and segregated in *Licania*, which is in line with our predictions. However, they were associated with (young) gaps only in *Licania*, the best disperser. Significant association of old seedlings with (old) gaps was only found in *Carapa*. However, we found no significant interaction of distance-to-gap and distance-to-adult for any of the species.

In case of *Carapa*, the latter might be due to the fact that none of the seed sources in the 4ha were standing along recent treefall gaps. Therefore, we compared the number of seedlings below adult trees between three trees in closed forest within the 4ha area and three trees standing along treefall gaps elsewhere in the 16ha area. The difference was tremendous (*t* test: $t_{2.04}$=-7.3, P=0.017): while 2, 1, and 0 seedlings were found below adults in closed forest, as many as 36, 38 and 54 seedlings <1m were counted below the adults along treefall gaps. A similar comparison for *Licania* showed no significant difference in numbers of seedlings below adults along gaps (4, 3, and 0 seedlings) and below adults in closed forest (1, 0, and 0). The majority of the *Carapa* seedlings below adult trees came from the 1998, a year in which abundant fruiting of several nut-bearing

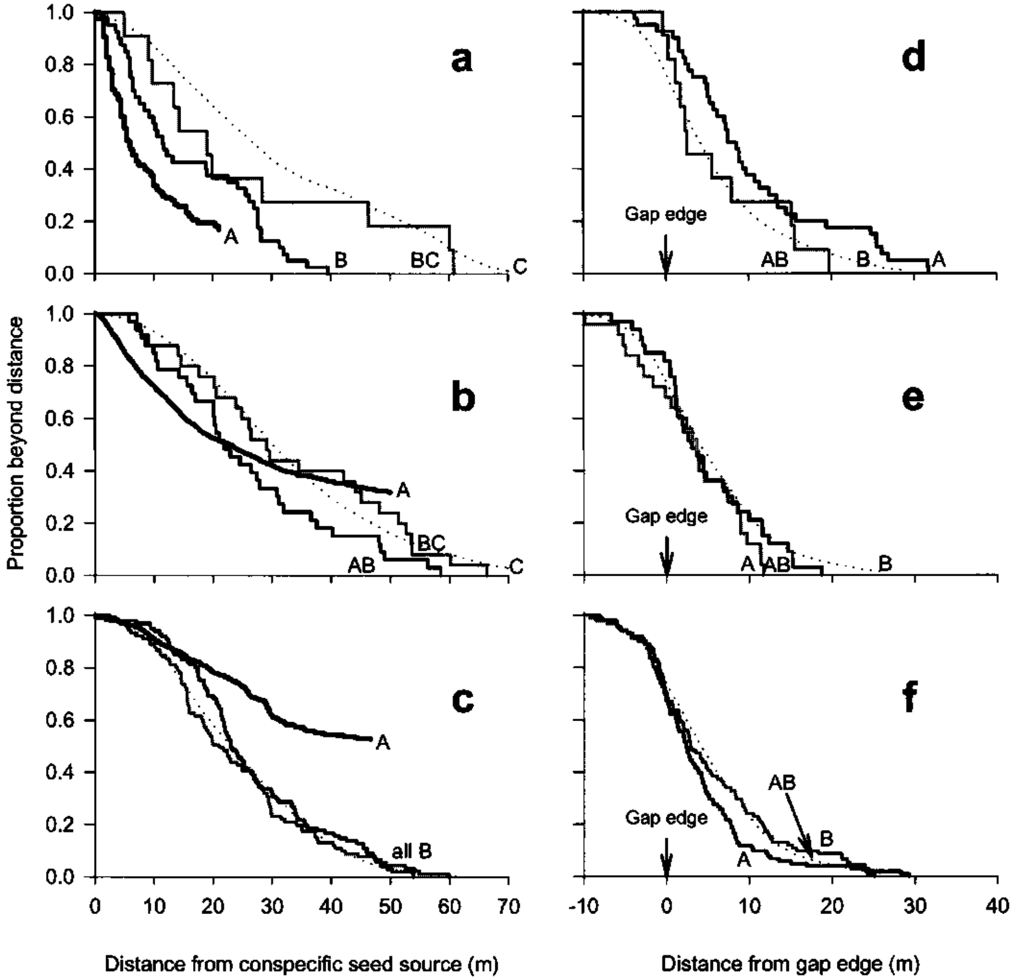

Figure 8.4 Spatial distribution of seedlings with respect to reproductive conspecifics (**a-c**) and treefall gap edges (**d-f**). Kaplan-Meier curves, showing the proportion of individuals further than a given distance, are plotted for young seedlings (black step functions), old seedlings (grey step functions), and random points (dotted lines). The thick lines (**a-c**) show the seed shadows as the proportion of seeds dispersed beyond a given distance from their original source. Characters indicate significant differences in pairwise Breslow (**a-c**) and Mantel-Cox logrank tests (**d-f**) at $\alpha=0.05$.

tree species saturated the seedeaters in the Nouragues area (CHAPTER 6). *Carapa* seed removal by rodents in that year was slow: seeds accumulated below seed sources and suffered heavy attack by granivorous insects. Still, many of those along treefall gaps germinated and established. *Licania* seeds in that same year, in contrast, were removed rapidly and did not accumulate below adult trees. Moreover, no post-shedding predation by insects seemed to occur. Without accumulation, there can be no contrast.

Table 8.2 Effect of distance to the nearest conspecific adult and gap on the probability of finding a seedling. Logistic regressions with seedlings versus 10,000 randomly generated non-occurrences. Figures are regression coefficients times 10^3. Positive values indicate association, negative values indicate segregation. There were no significant interactions of gap and adult proximity.

	Licania		*Carapa*		*Vouacapoua*	
	Young	Old	Young	Old	Young	Old
Distance to nearest						
gap 1996-1997	-22 **	-9 N.S.	-12 N.S.	33 *	-	-
gap 1993-1995	-11 N.S.	1 N.S.	-22 N.S.	4 N.S.	-	-
gap 1989-1992	-9 N.S.	2 N.S.	-2 N.S.	-40 *	25 N.S.	-8 N.S.
gap prior 1989	12 N.S.	16 N.S.	-22 N.S.	-56 *	-30 N.S.	-48 N.S.
conspecific adult	24 **	-1 N.S.	-32 *	-10 N.S.	-76 ***	-25 N.S.
Nagelkerke R^2 (%)	2.9	0.6	2.9	4.5	7.0	1.3

Significance values: *** $P<0.001$, ** $P<0.01$, *$P<0.05$, N.S. not significant.

8.4 Discussion

Both the escape hypothesis and the gap colonisation hypothesis have been positively tested in experimental studies for many tree species. Seeds and seedlings had greater survival in canopy gaps than in closed forest (e.g., Augspurger 1984; Howe 1990), greater survival away from reproductive conspecifics than underneath them (e.g., Augspurger 1983a, 1983b; Condit *et al.* 1994), and greater survival in isolation than in clumps of conspecific seeds or seedlings (e.g., Clark and Clark 1984). However, significant responses to experimentally created contrasts do not tell us how important these processes are for the natural spatial pattern of seedlings in which the majority of situations falls between these contrasts. Several studies, for example, report reduced survival at distances <5m from adult trees, but in most forests the area covered by this situation is negligible compared to the area available at distances >5m.

An approach that does permit inferences about the importance of these processes is to compare the natural spatial pattern of plants in different life stages, as in Augspurger (1983a) and this study. If distance- and density-dependent mortality and light-dependent survival were important for early survival of seeds and seedlings, distinct shifts away from adults and towards gaps should be visible in the distributions of seeds and seedlings. Our study compared the distribution of seeds, young seedlings and old seedlings for three rodent-dispersed tree species that differed in their extent of seed dispersal, and therefore the expected strength of density-dependent effect.

Our results gave support to the idea that dispersal helps seeds to avoid seed and seedling mortality associated with the proximity of conspecifics (escape hypothesis). The poorest disperser, *Vouacapoua*, showed a shift away from seed sources going from seeds to young seedlings to old seedlings. The frequency of seedlings, however, never became lower than expected from a random distribution. Distance-dependent mortality, at most, randomised the distribution of *Vouacapoua* seedlings. In contrast, seedling distributions of the better dispersers – *Carapa* and *Licania* – never differed from a random distribution.

Photo 8.1 Canopy gaps are very rich in light compared to understorey habitat.

Apparently low numbers of seedlings close to adults in these species were a sampling effect that disappears if one accounts for the availability of area at different distances from adult trees. This indicates that scatterhoarding by acouchies and agoutis can be an effective way to create a near-random distribution of seedlings in the forest. Transport away from the parent plant translates linearly into lower densities of seeds and thus seedlings. In *Carapa* and especially *Licania*, the scale of seed dispersal and scattering was apparently sufficient to avoid mortality associated with the proximity of reproductive conspecifics. The scale of seed dispersal in *Vouacapoua*, the less preferred species, was not. The effectiveness of seed dispersal by scatterhoarding rodents plays a crucial role for the expression of distance-dependent mortality.

None of the species showed clear effects of gap proximity, indicating that seedling survival was not strongly affected by light availability. Apparently, the large seed reserves permit seedlings emerging from forgotten caches to establish themselves and survive even under low light conditions for several years. High survival under low light is a known feature of large-seeded species (Saverimuttu and Westoby 1996; Walters and Reich 2000), but since all study species do better in gaps, the lack of a measurable effect of gap proximity was still unexpected. Rodents do not seem to disperse seeds into exposed situations such as recent gaps proportional to the availability gap area (P.A. Jansen, unpublished data), possibly because of higher predation risk in high light habitat. Recruitment, however, was very abundant below *Carapa* adult trees standing along recent treefall gaps but almost lacking below comparable adult trees surrounded by closed canopy. This demonstrates that seed and seedling survival can be quite high even right below adult trees if a treefall gap is present, which is in line with HYPOTHESIS 3 (Hammond and Brown 1998). High light conditions favoured establishment of seedlings, even though insects heavily predated upon the clustered and exposed seeds. Seedlings can mitigate losses of seed reserves to insects by high photosynthesis (Hammond and Brown 1998). Note that seedling recruitment below adult plants does not necessarily contribute to parental lifetime reproductive success, because parent-offspring conflicts may be at the cost of future seed production.

Our study assumed that seedlings come exclusively from seeds that are dispersed by scatterhoarding rodents. The high numbers of seedlings below *Carapa* trees along treefall gaps also show that recruitment from non-scatterhoarded seeds is also possible. Both burial and scattering of seeds by scatterhoarders are believed to reduce seed predation (Stapanian and Smith 1978; Vander Wall 1993). High light availability permitted *Carapa* seeds to germinate and establish in spite of high insect infestation. This supports the hypothesis that light availability is more important for reducing seed and seedling mortality than adult and sibling proximity (Hammond and Brown 1998). Nonetheless, scatterhoarding remains important for extending area, for increasing the probability of seeds hitting a gap or a site that will become a gap in the near future, and for helping seeds to escape seed predation and establish seedlings under low light situations. The same large seed reserves that persuade rodents to act as dispersers permit seedling survival in shade for a long time, waiting for gaps to arise.

Differences in food value seem to be the key factor for the species' ability to escape distance-related mortality. While many of the starchy, recalcitrant *Vouacapoua* seeds germinate before they can be removed from below parent trees (but see Forget 1990), the oily, slowly germinating *Licania* seeds are highly sought after by acouchies and agoutis that rapidly harvest all intact seeds from below parent trees to cache them. The removal rate of *Carapa* seeds is very much dependent on ambient food availability (CHAPTER 6). When many seeds are available including the preferred *Licania*, even the fatty *Carapa* seeds may accumulate below parent trees. The starchy, rapidly germinating seeds of *Vouacapoua* have relatively low value for acouchies and agoutis. By consequence, the animals harvest few of the seeds and spend little effort per seed in caching. Most seeds remain close to the parent tree in fairly high densities, yet the numbers of seedlings found near adult trees are low. In *Vouacapoua*, distance- or density-dependent mortality seems to shape the distribution of seedlings as predicted by the escape hypothesis (Connell 1971; Janzen 1970). In contrast, *Licania*'s highly nutritional, slowly germinating seeds are valuable to acouchies and agoutis. They put great effort in rapid harvesting and scatterhoarding the seeds in widely spaced caches to prevent discovery and use by food competitors. The resulting distribution of seedlings emerging from forgotten caches is completely random with respect to adult trees, with no sign of density-dependent mortality. *Carapa* seeds, finally, are sought after by rodents in the absence of the preferred *Licania* seeds. The investment in harvesting and scatterhoarding the seeds is intermediate between *Vouacapoua* and *Licania*, and so is the distribution of seedlings with respect to adult trees and gaps. In the presence of *Licania* seeds, *Carapa* seeds accumulate below parent trees where they are subject to density-dependent mortality factors that kill all except under high light conditions. Thus, the nutritional value of seed species and the availability of more attractive seed species determine the extent of seed dispersal by scatterhoarding rodents, and thereby the extent of seed and seedling escape from predators and pathogens.

Photo 8.2 Young *Licania alba* seedling, established from a seed cached along branches in a treefall gap by a scatterhoarding rodent.

8.5 Acknowledgements

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9. Synthesis

There is a great need of studies of seed dispersal that link seed production and seedling establishment, especially for animal-dispersed plant species (Wang and Smith 2002). This study filled this need for a nut-bearing tree species – the Neotropical rainforest tree *Carapa procera* – dispersed by scatterhoarding animals. It was among the first in tropical forest to track seeds from source to seedling establishment (*cf.* Chambers and MacMahon 1994; Vander Wall 1990). This study used video monitoring to identify which animal species were responsible for the harvesting of each individual seed, where other studies of seed dispersal by wild animals rely on assumptions about the identity of animals dispersing seeds (but see Hallwachs 1994; Beck and Terborgh 2002). I found that cavi-like rodents were the principal dispersers of nuts away from the parent neighborhood, as expected. However, dispersal was particularly by the Red Acouchy *Myoprocta exilis*, as in Forget (1990), rather than by the well-known agouti (*Dasyprocta* sp.) that is identified as principal disperser in most other Neotropical studies of scatterhoarding (e.g., Asquith *et al.* 1999; Hallwachs 1986, 1994; Meritt 1985; Peres *et al.* 1997; Smythe 1978).

9.1 Dispersal effectiveness

The tracking of dispersed seeds – using simple thread-mark techniques (Forget 1990) – showed that most of the seeds harvested by rodents were scatterhoarded, *i.e.* buried in spatially scattered single-seeded soil surface caches (CHAPTER 5-7). Most seeds remained within 25m from the source, but some were dispersed further than 100m away, which is much further than reported in other studies of scatterhoarding by rodents. Scatterhoarding brought seeds into more favourable conditions; seeds were distributed over a wide surface, thereby getting more isolated from conspecifics, they were buried out of reach of insect predators, and they were concealed for seed-eating mammals. Most seeds were recovered from caches, but subsequent seed tracking revealed that many recovered seeds were not consumed but re-cached, as in temperate studies of scatterhoarding (e.g., Vander Wall 1995; 2003; Vander Wall and Joyner 1998a). Re-caching could further increase the distance of seeds to the source and to conspecific seeds. A small proportion of the cached seeds ultimately germinated and established seedlings. This shows that scatterhoarding, even though performed by granivorous animals, was an effective dispersal mode for our study species.

The recognition that granivorous animals can be dispersers of seed rather than simply predators is fairly recent, and still growing. Even today, however, many authors equal seed removal to seed predation. They back up this assumption with the fact that some seeds were found eaten, and they ignore the possibility of scatterhoarding, or trivialise the likelihood of seedling establishment from cached seeds. And they can, because the idea of scatterhoarding being an effective dispersal mode has heavily relied on circumstantial evidence (CHAPTER 3). Because it is difficult and time-consuming to track seeds, very few studies have actually determined the ultimate fates of scatterhoarded seeds (e.g., Vander Wall 1994; 2002; Vander Wall and Joyner 1998). All, including this study, however, indicate that scatterhoarding provides effective dispersal and yield seedling establishment. Scatterhoarding can be a mutualism, benefiting both the tree that needs seed dispersal and the animal that cannot survive without seed supplies. Therefore, seed removal, especially of large seeds, should not be equalled to predation without verification.

9.2 Necessity of scatterhoarding

While some of the scatterhoarded seeds germinated and established seedlings, non-scatterhoarded seeds in the seed fate experiments all died from *Hypsipila* moth infestation, desiccation, or peccaries visiting seed trees (CHAPTER 6). The vicinities of parent trees functioned as zones of disproportionate mortality as described by (Janzen 1970) that seeds had to escape. Because rodents were the only vector of seed dispersal, most if not all seedlings of *C. procera* and other nut-bearing species found scattered throughout the forest (CHAPTER 8) must come from seeds cached by rodents. A recent study by (Asquith *et al.* 1999) showed that seedling recruitment in the large-seeded tree species *Hymenea courbaril* was dramatically lower in habitats without agoutis – the exclusive seed disperser (Hallwachs 1986) – than in places with this scatterhoarding rodent. Given the necessity of movement for the colonisation of new habitat and for migration in the face of climatic change over geological time, scatterhoarding is essential for the long-term subsistence of these tree species.

However, I also found that seeds accumulating below adult trees standing in or along treefall gaps did have a good chance to establish and survive (CHAPTER 8). High light availability in these situations compensated for losses of seed reserves to insect larvae (*cf.* Hammond and Brown 1998). The contribution of these seedlings to the population may seem unimportant given the low proportion of reproductive individuals standing in or along treefall gaps. But if one takes into account the high dynamics of the Guianan rainforest (Van der Meer 1995; Van der Meer and Bongers 1996), any given tree likely has one or more treefall gaps occurring in the immediate neighbourhood during its total reproductive life span. This provides windows of opportunity for in-situ replacement. Asquith *et al.* (1999), for example, also found at least some *Hymenea courbaril* seedlings below adult trees on islands without dispersers. This implies that nut-bearing species need not necessarily fail to reproduce in the absence of scatterhoarding rodents.

The question remains whether scatterhoarding rodents are essential for the regeneration of nut-bearing trees in disturbed forest, notably logged-over forest that is supposed to recover by natural regeneration. In CHAPTER 2, I reviewed the potential effects of logging on dispersal success and, ultimately, natural regeneration in tropical forest. One of the problems identified was that very little is known about the robustness of local regeneration to qualitative and quantitative alteration of animal-mediated dispersal. One cannot rule out the possibility that timber extraction and the subsequent uncontrolled hunting have a strong negative impact on regeneration of vertebrate-dispersed plants, including many timber species. I argued that, under current knowledge, forest management systems should better include effective protection of the disperser fauna. Is this also true for the scatterhoarding animals in our system?

Large seed dispersers are usually reduced in numbers in such forests due to uncontrolled hunting or habitat disturbance (CHAPTER 2). Acouchies, the main dispersers of *C. procera*, for example, are absent in disturbed forest in French Guiana (Dubost 1988). Add to this that seed sources are likely reduced in number due to logging of the largest individuals, fewer nuts will be dispersed. Whether and how poorer dispersal affects regeneration, however, will also depend on the compensatory effects of higher light availability (canopy disturbance) and lower population levels of seed predating mammals that are also hunted (CHAPTER 2). High light availability may result in high seedling recruitment from non-dispersed seeds below parent trees (CHAPTER 8), especially in absence of predation by peccaries, and in increased survival and growth of established seedlings. Finally, seedling recruitment will depend on scatterhoarder behaviour, which in turn is influenced by the ambient food abundance (CHAPTER 6). Dispersal might be reduced but nevertheless more effective due to increased cache survival, if the available food saturates the few available scatterhoarders at an earlier point. This suggests that recruitment of *C. procera* and other nut-bearing trees in managed forest need not be at risk even if dispersers have become scarce.

9.3 Dispersal quality

Like previous studies of scatterhoarding (e.g., Forget 1990), I found that many seeds were cached along logs, at the base of big trees, in litter piles below palms, and in the disturbed soil of treefall mounds and armadillo burrows. It has been suggested that agoutis and acouchies use these objects as mnemonics, like many other scatterhoarding species do (e.g., Barkley and Jacobs 1998; Bossema 1979). CHAPTER 3 proposed the alternative explanation that these places have substrates – such as mouldered wood and leaves – in which cache thieves less easily detect caches. An artificial experiment in which I simulated seed caches in different substrates (not reported in this thesis) supported this idea. Caches in mouldered wood or other loose substrates had lower pilferage rates than caches in clayey soil, the prominent substrate. Further artificial caching experiments showed that digging traces were the primary cue for cache thieves, far more important than cache content. Mammals explored artificial caches containing worthless seeds or even nothing at all with the same enthusiasm as high-value caches. I propose that rodents prefer caching seeds in places / substrates that allow burial with little disturbance as to minimise cache robbery. Seed caching in such places may also be cheaper for animals in terms of energy expenditure. This implies that there are different qualities of places to cache seeds, on which I will elaborate in the next section.

I reasoned that recent gaps would be a particularly suitable environment for caching seeds because logs, branches and liana tangles obstruct peccaries, which are considered important cache robbers (Kiltie 1981). Also, treefall gaps are rich in leaf accumulations and decaying wood, substrates that, as explained above, allow safe caching. Artificial caches created in recent treefall gaps indeed had greater survival than artificial caches in understorey. However, cache survival did not differ between old treefall gaps and open understorey (unpublished data). This suggested that cache robbers avoided the high light environment. That acouchies and agoutis did so was also suggested by the fact that natural caches in our seed fate experiments were rarely in recent treefall gaps (unpublished data). A plausible explanation is a higher risk of predation, for example by the bush master *Lachesis muta*. This snake feeds on small mammals including acouchies and agoutis, and prefers high light conditions for roosting.

Light availability is a limiting factor for growth and survival in nut-bearing species as in any other, yet cached seeds as well as established seedlings were mostly found in understorey habitat (CHAPTER 8; unpublished data). The benefit of scatterhoarding is apparently not in directional dispersal towards existing gaps, but rather in spatial scattering over a wide area. The over-dispersion of cached seeds maximises the probability that seedlings are present whenever and wherever a canopy gap arises. It may not be far from ideal dispersal, which produces seedlings at the spatial scale of treefall gap occurrence. Anticipating future gaps requires that seedlings be vigorous enough to survive in the dark understorey conditions for several years. Large seeds are often interpreted as an adaptation for this (e.g., Leishman and Westoby 1994), and I found in greenhouse experiments with *C. procera* and *V. americana* (unpublished data) that seed size translates into seedlings with greater leaf area and a greater capacity to survive heavy damage or herbivory. Especially *V. americana* have high survival rates in understorey habitat, more so than *C. procera* (Forget 1997). The large seed size in nut species is suited not only for dispersal by scatterhoarding rodents, but also for the conditions into which dispersal brings seeds.

9.4 Escape of cached seeds

Nuts can escape consumption by scatterhoarders by establishing seedlings and become unattractive as food. However, the road to establishment – germination – is dangerous, because the rodents actively manage their supplies. I found that *C. procera* seeds were especially prone to recovery at emergence of the sprout (CHAPTER 5-6). Rodents used these sprouts either as cues for cache retrieval, or as a signal of seed reserves leaking away. I found that they actively intervened in germination by severing sprout, roots and meristem (CHAPTER 4), and that they subsequently re-cached most of these seeds (CHAPTER 6). Seeds that received this treatment were unable to germinate again but stayed alive in secondary caches for several months, long enough to serve as food during the dry season. The animals thus changed rapidly germinating and therefore perishable seeds into long-term food supplies.

Because scatterhoarding rodents and the *Carapa* germination type co-occur worldwide, I hypothesised that the phenomenon of 'zombie seeds' is widespread (CHAPTER 4). But if the zombie phenomenon were widespread, then why have studies of seed damage and seedling herbivory never reported it? A plausible explanation is that these studies focus on damage to seeds by granivores príor to germination, and/or on damage to sprouts by herbivores and mechanical causes áfter germination. They test whether seeds germinate after experimental damage and/or whether seedlings resprout after experimental removal of the shoot (Andersson and Frost 1996; Dalling *et al.* 1997; Harms and Dalling 1997; Hoshizaki *et al.* 1997), but never test the resprouting ability of seeds after removal of the entire seedling. At first glance, the characteristic of becoming zombies after seedling removal seems a handicap that may strongly reduce seed survival and, ultimately, plant reproductive success. However, the 'handicap' of becoming zombies may actually be the only reason why scatterhoarding animals use these perishable seeds for long-term hoarding rather than instant consumption. If only a proportion of scatterhoarded seeds escape the rodents' attention, dispersal success may already be sufficient.

By scattering caches over a wide area, acouchies made it more difficult for food competitors to find and deplete the supplies (CHAPTER 5), as predicted by (Stapanian and Smith 1978). Negative density dependence of cache depletion by naïve foragers was even more clearly shown when *C. procera* seeds were experimentally scatterhoarded in different densities to test for related differences in cache survival time (unpublished data). However, the scattering turned against the acouchies when caches became numerous and the animals simply lost track of the seeds. This happened especially in years of seed abundance. Most cached *C. procera* seeds escape consumption because their dispersers are apparently unable to timely intervene in the rapid germination (CHAPTER 6).

The other mechanisms of cache survival described in CHAPTER 3 – notably memory loss over time and high scatterhoarder mortality – may still be important in slowly germinating nut species, such as *Licania alba* and various palm species. Yet, even in these species the same game begins once cached seeds germinate and emerging sprouts give away their hide. If acouchies recognise *C. procera* seeds by their sprouts, they likely recognise other palatable seed species by their sprouts as well. Thus, reasoning that it is dangerous for palatable seeds to germinate when seeds are sought after, one may expect that germination time of nut species be tuned to ambient seed availability and have their sprouts be swallowed up in the crowd of seeds.

9.5 Seed size

Seeds of scatterhoarder-dispersed tree species can be several orders of magnitude larger than those produced by tree species dispersed by wind or fruit-eating animals (e.g., Leishman *et al.* 1995; Westoby *et al.* 1996) (FIGURE 9.1). Smith and Reichman (1984) hypothesised that this large-seediness has evolved in response to preferences of scatterhoarding animals. This study used the 20-fold variation in seed mass of *C. procera* to study the effect of seed size on scatterhoarding, without confounding variables, and found that larger seeds were indeed given a more favourable treatment than smaller seeds. Large seeds were more likely removed and scatterhoarded, dispersed further away, and cached in lower densities (CHAPTERS 5 and 6). The result was that large seeds were more likely to establish seedlings than small seeds.

Several empirical studies have now shown that the effectiveness of dispersal by scatterhoarding animals can increase with seed size (e.g., Vander Wall 2003; this study). Superior dispersal for larger seeds is in line with optimal foraging theory: greater food value makes larger seeds more attractive to seedeaters and merits a greater expenditure in caching. The findings, however, are opposite to the established idea that dispersability decreases as seeds get larger (e.g., Baker 1972; Stanton 1984; Howe and Westley 1986; Levey 1987; Hedge *et al.* 1991; Mack 1993; Jordano 1995; Westoby *et al.* 1996). Nut-bearing plants challenge the paradigm that dispersability is traded-off against vigour.

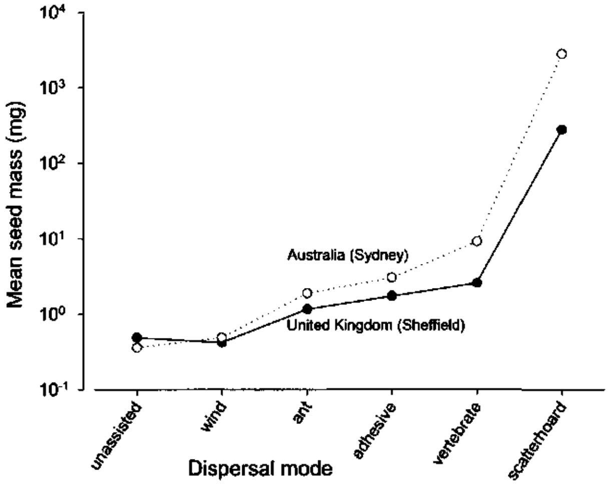


Figure 9.1 Average seed mass (log-scale) for different dispersal modes in two floras. After Leishman *et al.* (1995).

Clearly, even dispersal by scatterhoarding animals cannot increase with seed mass infinitely: there are limits to the size and mass of seeds that any scatterhoarding animal can carry given its own mouth width and body mass. I therefore hypothesised that an optimum seed size exists for seed dispersal by any given scatterhoarding animal species. Closer consideration of scatterhoarding by specifically acouchies revealed that these animals indeed gave the most favourable treatment to intermediate-sized seeds (CHAPTER 7). A corresponding trend was found for White-tailed rats in Australia (Theimer 2003). This suggests that selectivity of scatterhoarding animals leads to stabilising selection on seed size rather than directional selection towards ever-larger seeds.

9.6 Predation versus dispersal

There is great disagreement in the existing literature on the effect of seed size on the probability of seed predation (instant seed consumption) and scatterhoarding (delayed and incomplete seed consumption) by granivorous vertebrates, particularly rodents. The majority of published studies of seed predation and seed size report that seed predation increases with seed size (e.g., Crawley 1992; Hulme 1998; Janzen 1971; references therein). In contrast, this dissertation and other recent studies show that large seeds are more likely cached by scatterhoarding animals than small seeds (CHAPTERS 5 and 6 and references therein). But, there is also one study (Brewer 2001) that found the inverse for palm seed scatterhoarding by spiny pocket mice. Moreover, large *C. procera* seeds were favoured only up to a certain point beyond which seed caching became increasingly difficult (CHAPTER 7). Theimer (2003) also found a similar tendency of intermediate-sized seeds being favoured by scatterhoarding White-tailed rats in Australian rainforest. How can these contrasting results be explained?

One possibility is that the suitability of seeds for consumption by scatterhoarding animals and the suitability for scatterhoarding (delayed consumption) are not dependent on seed size in the same manner. Seed sizes suitable for scatterhoarding likely are a limited subset of the seed sizes that are suitable for consumption. This would imply that some seed sizes are both dispersed and predated upon by a given granivore, whereas other sizes experience only seed predation. CHAPTER 7 suggested that there are two threshold sizes for scatterhoarding: a size below which seeds are unattractive for scatterhoarding, because the costs of hoarding are greater than the benefits, and a seed size beyond which scatterhoarding is physically impossible. Moreover, there was an intermediate seed size at which scatterhoarding was most likely and provided the furthest dispersal. We can now subdivide the range of seed size into three zones in which scatterhoarders have a different impact:

(1) Seeds smaller than the threshold size for scatterhoarding experience only seed predation. As seed attractiveness as food increases with seed size, so will seed predation. This may be the range of seed sizes in studies of small seeds that find higher predation for larger seeds (e.g., Crawley 1992; Hulme 1998).
(2) Beyond the size at which seeds become suitable for scatterhoarding, seeds experience both dispersal and predation. Up to the optimum seed size for scatterhoarding, the likelihood of seed dispersal (instead of predation) increases with seed size. This is the range of seed sizes of studies of scatterhoarding that find better dispersal for larger seeds (e.g., Bossema 1979; Forget *et al.* 1998; Hallwachs 1994; Vander Wall 2003; CHAPTER 5-6).
(3) Finally, beyond the optimum seed size for scatterhoarding, the likelihood of seed predation (instead of dispersal) again increases with seed size. Beyond the point at which seeds become too large to be scatterhoarded, seeds even experience only seed predation, just like small seeds. This may be the range of seed sizes in studies of large seeds that find higher predation for larger seeds (e.g., Alcantara *et al.* 2000; Brewer 2001).

Seed predation has a tremendous impact on the survival and distribution of seeds (Crawley 1992) and the degree of seed predation is clearly influenced by seed size. If the idea outlined above holds, there would be two regimes of selection on seed size due to seed predation by a given scatterhoarding species. For seeds that are too small to be scatterhoarded, selection is directional towards smaller seeds. This will be up to a point at which seeds become too small to serve as food, for instance because they do not permit a sufficiently high rate of food intake, and are no longer affected by the scatterhoarder at all. For larger seeds, in contrast, selection is stabilising towards an optimum seed size for scatterhoarding, as suggested in CHAPTER 7. These two different regimes may perhaps explain the dichotomy in seed size that exists between plant species dispersed by scatterhoarding animals and species dispersed by various other modes (FIGURE 9.1).

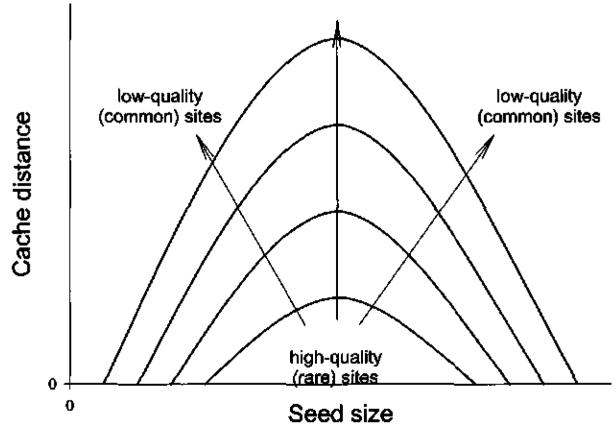


Figure 9.2 Predicted difference in quality of caching sites among scatterhoarded seeds. The drawn lines are hypothetical iso-quality lines of caches. The quality of caches in the core of the distribution diagram is greater than the quality of caches placed along the edges (*cf.* FIGURE 7.1C).

9.7 Cache spacing

I found that the average distance at which rodents cached seeds increased with seed mass (CHAPTERS 5-6) or rather with seed value (CHAPTER 7). This result was in line with optimal cache spacing theory (Clarkson *et al.* 1986; Stapanian and Smith 1978), predicting that scatterhoarders spend more effort on caching more valuable items, the most valuable items in our study being the intermediate-sized seeds. However, optimal cache spacing theory specifically predicts that an optimum cache density exists for each seed value, and thus a corresponding optimum transport distance and energy expenditure.

I found no support for this idea. Rather than just the average dispersal distance, the range of dispersal distance increased with seed value, resulting in a so-called envelope effect (Cade *et al.* 1999; Scharf *et al.* 1998) (CHAPTERS 5-7). In other words, low-value caches were always found within a narrow range of few meters from the source, whereas high-value caches were found at distances ranging from few meters up to more than 100. I also found that the isolation of caches was a by-product of dispersal distance, with no additional variation explained by seed mass (CHAPTER 5). In other words, given a certain dispersal distance, more valuable seeds were isolated from other caches not more than were less valuable seeds. These findings suggest that another mechanism be operating.

A possible alternative explanation for these patterns is that animals select caching sites based on their quality as hiding place, rather than on their density. Site quality may for instance be connected to more or less concealing substrate (SECTION 9.3). Scatterhoarding animals are known to select cache sites as to reduce the probability of robbery by cache thieves (Vander Wall 1990; references therein). Steven (cited in Vander Wall 1990), for example, showed that marsh tits (*Parus palustris*) learned to avoid caching seeds in a particular substrate from which the experimenter systematically removed seeds. Now suppose that there are different qualities of caching sites, as suggested in

SECTION 9.3, and that high-value seeds require more careful hiding – *i.e.* a safer hiding place – for cache thieves than low-value seeds, as in optimal cache spacing theory (Clarkson *et al.* 1986; Stapanian and Smith 1978). While any quality sites will do for caching low-value seeds, high-value seeds require high quality sites, which are a limited subset of all available sites. Now, while density is a function of dispersal distance (a lower density requires further dispersal), site quality is stochastic. This means that it may take an acouchy several minutes of walking to find a site that meets its quality demand, but it may all the same take only seconds, if a suitable site happens to be available right near the source. The range of possible search times, reflecting the uncertainty margin, increases with the desired minimum site quality and thus with seed value. Such stochasticity might produce the heteroscedastic variation in cache distance observed in CHAPTERS 5-7. A corresponding testable hypothesis is that high-value seeds, given a certain distance or density, are cached in higher-quality sites (substrates) than low-value seeds.

Of course no animal can uphold a high site quality demand forever. Scatterhoarders must get rid of seeds before the costs of searching and caching outweigh the expected benefits. This might imply that an animal that is unsuccessful in cache finding will gradually lower its site quality demand over time, and will ultimately even cache seeds in low-quality sites if it has not been successful in finding any better. Not only must it do so because the seed does not allow a greater investment, it also can afford doing so because dispersal away from the source provides additional protection against cache thieves, as it increases the isolation from other seeds (CHAPTER 5). Cache density or isolation, however, is not actively manipulated by the scatterhoarder. A corresponding testable hypothesis is that (high-value) caches in the core of the seed distribution (FIGURE 7.1C) are at higher-quality sites than caches near the edge (FIGURE 9.2). Moreover, a seed may be cached further away as scatterhoarding takes place later because suitable caching sites in the vicinity gradually become depleted (SECTION 9.4). The further dispersal of seeds in larger cafeteria plots (CHAPTER 6; unpublished data) supports this idea. This would imply that trees can to some degree increase dispersal distance not only by seed value but also by seed number, bigger crops requiring a greater area for storage.

9.8 Species specificity

CHAPTER 7 introduced the idea that an optimum seed size exists for scatterhoarding by a given species, which I further elaborated upon in SECTION 9.6. Which size is optimal should be species-specific, and be dependent on, amongst others, the dimensions of the animal species. Body size and mouth widths determine beyond which seed size the handling and scatterhoarding of seeds becomes too difficult for an animal and ultimately impossible. Agoutis, for example, are able to carry larger seeds than the smaller acouchies. Moreover, the size at which seeds are big enough to be attractive for hoarding will depend on animal dimensions as well. Thus, the optimum seed size for a nut-bearing plant species will depend on the scatterhoarding species with which it interacts.

Most nut-bearing species, however, do not interact with a single scatterhoarding species but with several, which differ in body size and their responses to seed size. Nuts in Guianan rainforest, for example, are scatterhoarded by agoutis, acouchies and spiny rats, which weigh, on average, 4.0, 1.3 and 0.5kg, respectively. And acorns in European forests are scatterhoarded by jays (Bossema 1979) and woodmice (Den Ouden 2000), weighing 145-185g and 20-30g, respectively. Moreover, seed species interact with different sets of scatterhoarder species throughout their area. *C. procera*, for example, occurs throughout the Amazon rainforest, with different rodent communities, but also in Western Africa, where large rodents are absent. Finally, seed species interact with varying sets of animal species over evolutionary time (Vander Wall 2001).

Smith and Reichman (1984) hypothesised that the large-seediness of nut-bearing trees has evolved in response to preferences of scatterhoarding animals, and my results supported a major underlying assumption. But how can plants adapt to scatterhoarding animals if there are several optimum seed sizes that also vary in time and space? A theoretical possibility is coevolution of seed size with disperser assemblage. If this takes place, it should be visible in a species as widespread as *C. procera*. Its African populations should then have markedly smaller seeds than Neotropical ones. And the species should also display geographical variation in seed size within the Neotropics, with the largest average seed size produced in places where acouchies are absent and agoutis are the principal dispersers.

Another possible way to cope with the unpredictability of dispersers is through generalism. By maintaining a certain amount of variation in seed size, species can increase the likelihood of having at least some seeds in the size range suitable for scatterhoarding by the available dispersers. By targeting different dispersers, the species is less likely to become evolutionary 'trapped' (*sensu* Schlaepfer *et al.* 2002). The amount of seed size variation in the widely distributed *C. procera* is indeed huge, which was why I chose this species in the first place. Most other nut-bearing tree species display far less variation. The question arises whether nut-bearing tree species with wide variation in seed mass tend to have a wider distribution area with more variation in disperser assemblages than species with little variation.

9.9 Mast seeding

CHAPTER 6 tested the idea that mast seeding stimulates scatterhoarding seedeaters to act more as dispersers and less as predators of the seeds they harvest, in line with the predator satiation hypothesis (Janzen 1974) and earlier ideas of predator swamping in animal ecology (e.g., Kruuk 1972). My seed fate experiments covered five consecutive years that varied in seed abundance: Three years had abundant fruiting, two had fruit scarcity. I found that cached seeds were indeed more likely to escape consumption by rodents and peccaries and to establish seedlings in years of seed abundance. Scatterhoarding rodents were more effective dispersers, and the granivore community as a whole were less heavy seed predators under seed abundance than under seed scarcity. I also found that dispersal quality increased with crop size (CHAPTER 6; unpublished data), which agrees with the idea that seeds must be stored further away as the area near the source gets filled up with caches (Clarkson *et al.* 1986; SECTION 9.5).

I also found that seed abundance strongly influenced scatterhoarder selectivity. Saturation in years of seed abundance made the animals highly selective, whereas hunger made the perfect sauce for low-value seeds in poor years (CHAPTER 6). This implied that seed selection was determined not only by seed nutritional content but also by

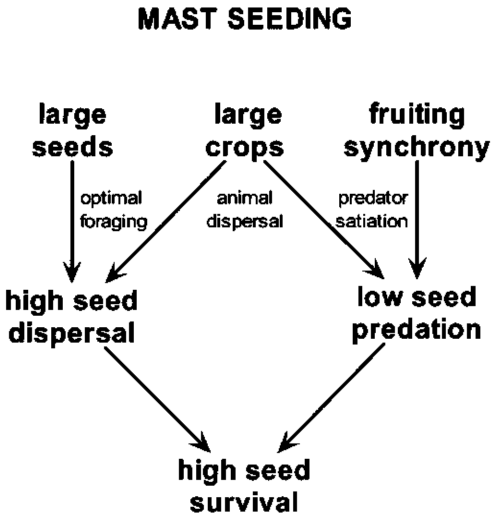


Figure 9.3 General model for mast seeding in nut-bearing plants. The arrows indicate hypothetical causal relationships. See text and CHAPTER 6 for further explanation.

seed scarcity. Seed abundance not only increased the discrimination by rodents on seed size within species, but also the discrimination among species. For example, *Eugenia* and Sapotaceae seeds were rapidly harvested and scatterhoarded in 1997, a year of food scarcity, but were completely ignored in 1998, a year with abundant fruiting of preferred species such as *C. procera* and *L. alba* (unpublished data). These findings underline that the circumstances under which seed fate experiments are carried out greatly influence the outcome, which must certainly be taken into account when comparing experiments.

There are limits to the reproductive effort any individual can make due to nutritional and physical constraints. Smith and Fretwell (1974) hypothesised that these limits imply that seed size and seed number are traded-off, and that plant species must find an optimal balance between producing big seeds and producing many. My findings suggest that nut-bearing trees can maximise scatterhoarding and minimise seed predation by producing large crops simultaneously with other nut-bearing trees in the population (CHAPTER 6). At the same time, they must produce pretty big seeds to maximise the chance of scatterhoarding rather than instant consumption (CHAPTERS 5-7). And the necessity of producing high-value seeds is even greater under seed abundance, when competition for dispersers is fierce (see above). Mast seeding, the production of large synchronous crops of large seeds in alternation with several small crops, seems a perfect solution. Rather than trading off seed size and seed number within crops, mast-seeding trees trade-off resources between consecutive crops, displaying large and large-seeded crops in some years at the cost of crops in other years.

How mast seeding in nut-bearing trees is related to seed dispersal and predation is summarized in FIGURE 9.3. The diagram is based on the earlier, more general model by Sork (1993). Seed abundance swamps the local community of seedeaters with food. Scatterhoarding animals respond to seed abundance by acting as seed dispersers more and less as seed predators (CHAPTER 6). Moreover, large seed size stimulates scatterhoarding, and more so under seed abundance (CHAPTER 5-6). And synchronisation of high-production years among the population, by responding to the same physiological trigger, makes it impossible for seed-eating mammals to adapt their population levels to the peaks of seed availability. The idea of mast-seeding trees trading-off resources between consecutive crops could be tested by comparing post-fruiting mortality between masting and non-masting species.

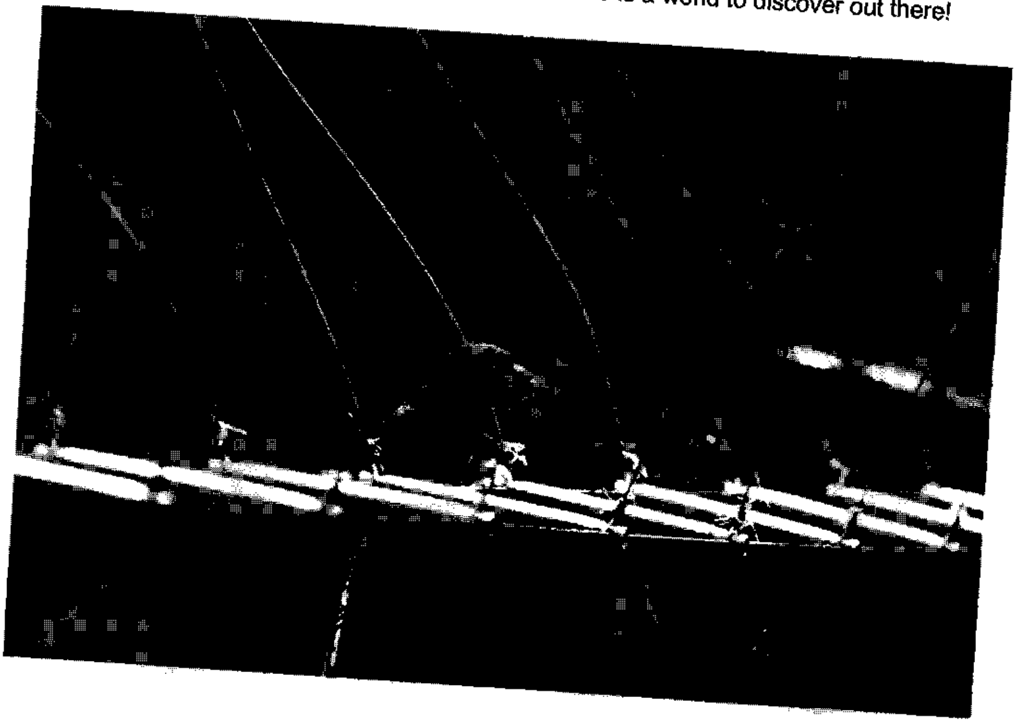
9.10 Perspectives

The field of seed dispersal is at the point of breakthrough. New methods have become available to facilitate or avoid the tracking of seeds that has hampered studies of ultimate seed fate to date (Wang and Smith 2002). The most powerful of these are perhaps the *various molecular techniques that allow us to evaluate dispersal success at different* spatio-temporal scales, from continental dispersal over geological time (McCauley 1995) to local dispersal from seed source to growth site (Godoy and Jordano 2001). Scatterhoarder-dispersed plant species are particularly suitable for the latter, more detailed studies. Not only can dispersed seeds be matched with mother trees by endocarp nuclear DNA, which is 100% maternal and highly variable, enabling us to uncouple pollen and seed dispersal (Godoy and Jordano 2001). Even established seedlings, the successful offspring, can be matched because we can extract endocarp nuclear DNA from the remains of the buried seed from which these seedling established. We can thus trace back the dispersal process, avoiding the many difficulties of tracking a seed cohort that shrinks over time so strongly that huge sample sizes are required, as in the experiments in this dissertation. These techniques may greatly help to investigate the effects of seed size and seed number on the probability of seedling establishment. One could, for example, use the seed remains of established seedlings to estimate their original seed size, and evaluate whether a particular size established further than others. Or one could compare the size distribution of seeds produced by a given tree with that of its successful offspring, and evaluate whether the latter are a non-random subset of all available seed.

To really understand seed dispersal by scatterhoarding animals, it remains essential to study the process itself. Here too, new techniques shall make life easier or at least more exciting. The detailed study of foraging behaviour has come within reach of many researchers now compact digital consumer cameras have become available, including advanced functions such as night vision, time-lapse mode, time indication and external triggering. Monitoring seed removal with this equipment will be much easier and cheaper than with the bulky surveillance equipment that I used.

A promising new technique are large-scale telemetry systems such as installed at Barro Colorado Island (BCI), Panama. This permanent multi-receiver system makes it possible to simultaneously track – in real time – the movements of large numbers of radio-tagged animals. But why not radio-track seeds tagged with transmitters that switch on when they move? Simultaneously radio-tracking seeds and dispersers (agoutis at BCI) could solve unanswered questions such as whether caches are pilfered by their owners or by cache thieves, depending on the places where they were made.

A powerful experiment that I could not do because the Nouragues study site is a strictly protected reserve, is to experimentally remove or replace scatterhoarding animals after they have built up a supply of seeds and see how this affects seedling recruitment. Greater numbers of seedlings should emerge if these animals rely on memory for cache retrieval. If so, this would imply that the probability of seedling recruitment may increase with the abundance of cats and other predators of scatterhoarders. Just one step further are experiments in which portions of habitat are enclosed within which the abundance of seed, scatterhoarders, and seed predating mammals are manipulated to disentangle the mechanisms that make seedeaters help trees. There is a world to discover out there!



Summary

This dissertation studies the dispersal and predation of large seeds by scatterhoarding animals. Seed dispersal is the movement of seeds away from the parent plant, whereas, seed predation is the killing of seeds by animals that feed on them. Scatterhoarding is the hiding of food in numerous spatially scattered caches with little food each, with seed dispersal as a by-product. Animals that hide seeds do so to create food reserves that they can draw upon in subsequent periods of food scarcity, such as winters in the Temperate Zone and the dry season in many tropical forests.

I studied scatterhoarding of nut-bearing tree species by large cavi-like rodents in the undisturbed tropical rainforest of Nouragues, French Guiana, South America. These rodents – agoutis and acouchies – hide seeds, one by one, in shallow soil surface caches with a single seed each. The scatterhoarding takes seeds away from the parent trees, isolates them from conspecific seeds, protects them against granivorous insects and vertebrates, and plants them in the soil. Potentially, this treatment is favourable for seed survival and seedling establishment, but only if the scatterhoarder, for whatever reason, does not recover the seed for consumption. The big question is whether the seed dispersal part of scatterhoarding counterbalances the seed predation part, and how plant traits such as seed size, crop size and fruiting phenology influence this balance.

I linked seed production and seedling establishment – dispersal success – by tracking thousands of seeds individually over the course of the scatterhoarding process. I used video surveillance to record which animal species removed individually numbered and thread-marked seeds from cafeteria plots. Subsequently, I tracked the seeds to see what happened to them. Threadmarks protruding from the soil gave away the hide of buried seeds. I varied seed size but not species within the cafeteria plots, and did this in several consecutive years that differed in seed abundance, to see how scatterhoarding was affected by seed size and seed abundance.

My study had three goals. The first was to determine whether scatterhoarding is an effective dispersal mode, yielding established seedlings. This study is needed to take away the doubt about the role of scatterhoarding rodents in the forest ecosystem, as the idea of effective dispersal by these animals heavily relies on circumstantial evidence. The second was to determine whether nut-bearing trees depend on scatterhoarding for regeneration. This was needed to find out whether the recruitment of these species would be at risk in managed forests where the fauna is not protected. The third goal was to determine how seed size and seed abundance influence the dispersal effectiveness of scatterhoarding. This was intended to test the idea that feeding responses and preferences of scatterhoarding rodents had caused the evolution of large seeds and mast seeding in nut-bearing trees.

After a general introduction (CHAPTER 1), the dissertation starts with a general review about seed dispersal in rainforest ecosystems and on the potential effects of logging on dispersal success and, ultimately, natural regeneration (CHAPTER 2). One of the problems identified is that very little is known about the robustness of local regeneration to qualitative and quantitative alteration of animal-mediated dispersal. Timber extraction and uncontrolled hunting following road building may have a strong negative impact on regeneration of vertebrate-dispersed plants, including many timber species. It is argued that, under current knowledge, sustainable forest management should include effective protection of the disperser fauna.

CHAPTER 3 introduces the dispersal system studied in this thesis with a review of seed dispersal by scatterhoarding animals, and many examples from three nut-bearing tree species in Guianan rainforest. This chapter explains what scatterhoarding is, why it is important for animals, and why it is though to be important for certain plant species, especially for large-seeded trees. It aims to present a state-of-the-art, identifying the lacunas in present knowledge and outlining some hypotheses that need to be tested.

The remainder of this thesis is devoted to actually testing some of the plant-centred hypotheses introduced in CHAPTER 3, using one of the three tree species, *C. procera*, whose seeds are much sought after by scatterhoarding rodents. CHAPTER 4 asks the question of why scatterhoarding rodents would be interested in hiding these seeds at all: Rapid seed germination characteristic for *C. procera* likely depletes seed reserves before the rodents need them. The results of a series of experiments show that the rodents actively intervene in germination by removing the embryo, thereby creating seed reserves with sufficient storage life to serve as food supply for the dry season. Thus, the rodents change perishable seeds into reliable long-term supplies.

The next three chapters present results from the seed fate tracking experiments in which I used video cameras and threadmarks to follow the fate of *C. procera* nuts. All are about the consequences of rodent feeding preferences for seed predation, dispersal and, ultimately, seedling establishment. Plant species that depend on scatterhoarding animals for seed dispersal have comparatively large seeds. An intriguing hypothesis to explain this is that large-seediness has evolved as a result of selectivity by scatterhoarding animals, which would preferentially scatterhoard large seeds. CHAPTER 5 is a test of the major assumption underlying that idea: rodent scatterhoarding behaviour favours large seeds over small ones. I followed the fate of seeds that greatly varied in seed mass yet not in species. The probability of establishing was negligible for small seeds compared to large ones, suggesting that scatterhoarders indeed cause selection towards large seeds. Thus, nut-bearing plant species challenge the paradigm that dispersability is traded-off against vigour. The distribution pattern of caches was strongly dependent on seed size, but not in the way predicted by existing theories. Quantile regression analyses showed that not only the average dispersal distance increased with seed mass, but so did the range of dispersal distances. The results also show that seedling establishment from scatterhoarded seeds indeed occurred, even under the food scarcity during which the experiment took place.

A spectacular phenomenon shared by many plant species with dispersal by scatterhoarding animals is *mast fruiting*: the alternation of years with modest or no fruiting with years of abundant and synchronous fruiting. CHAPTER 6 tests one of the oldest and best-established functional explanations for mast seeding, the so-called 'predator satiation' hypothesis. It argues that massive fruiting in masting years overwhelms seed predators so seed survival can be relatively high, while intermediate years of poor fruiting prevent seed predators from reaching a population level that fits the food abundance in masting years. I compare rates of scatterhoarding and cache exploitation between three years of poor and two of abundant fruiting. I also test the hypothesis emerging from CHAPTER 5 that seed mass affects dispersal more strongly in rich years than in poor years. The results demonstrate that reproductive success in rich years is indeed much higher, even though the rates of scatterhoarding are much lower, and that scatterhoarding also favours large seeds more in rich years. Large seeds in large crops produced under seed abundance have the highest probability of seedling establishment from caches.

The two previous chapters tested the idea that the scatterhoarding behaviour of rodents would favour larger seeds. Reasoning that there must be a seed mass or size beyond which rodents can no longer carry seeds, CHAPTER 7 tests whether scatterhoarding favours some intermediate seed size rather than ever-larger seeds. The results show that acouchies indeed give the most favourable treatment to intermediate-sized seeds rather than the largest available. This suggests that scatterhoarding animals cause stabilising selection on seed size rather than directional selection to ever-larger seeds.

CHAPTER 8 considers the result of dispersal, the spatial pattern of successfully established seedlings. For three nut-bearing tree species, as introduced in CHAPTER 3, which differ in the extent of scatterhoarding. I compare the seed shadows and distributions of young and old seedlings with respect to reproductive conspecifics and treefall gaps. Three ideas are tested. The first – the escape hypothesis – predicts disproportionate seed and seedling mortality near reproductive conspecifics. Only the poorly dispersed species showed the predicted pattern. Dispersal in the two better-dispersed species seemed effective in avoiding these effects. The second – the gap colonisation hypothesis – predicts disproportionate seedling survival near and in treefall gaps. This effect was not found in any of the species, probably because the large seeds enable seedling survival independent in deep shade. That none of the species was more common in light gaps is probably also because scatterhoarding animals avoided high light habitats. The third idea – that light availability is more important for seedling survival than distance to reproductive conspecifics – predicts that seedlings may even establish near reproductive conspecifics even only there is enough light available to compensate for seed reserve losses to insects. This prediction was confirmed for *C. procera*. I conclude that scatterhoarding is an effective way for seeds to escape parent-related mortality but not to reach existing canopy gaps. Rather, the scattering of seeds and the longevity of these large-seeded seedlings in deep shade increase the likelihood that a seedling is present wherever and whenever a treefall gap arises.

CHAPTER 9 is a synthesis of the findings, including some results of experiments not reported in this dissertation. It is concluded that scatterhoarding is an effective dispersal mode for nut-bearing plant species, which can yield reasonable numbers of established seedlings (*cf.* QUESTION 1). I also conclude that *C. procera* depends on scatterhoarding for long-term subsistence in the forest ecosystem. However, seedling recruitment in managed forest seems not at immediate risk if scatterhoarding rodents become scarce, especially because the more frequent high light conditions increase seed and seedling survival (*cf.* QUESTION 2).

The likelihood and quality of dispersal by scatterhoarding animals increases with seed size (*cf.* QUESTION 3), but only up to a certain size beyond which seeds become difficult to manipulate, resulting in an optimum seed size for dispersal by a given scatterhoarding species. The optimum size and the seed size range suitable for scatterhoarding are likely scatterhoarder-specific, depending on body and mouth size. Because nut-bearing plant species interact with different assemblages of scatterhoarding species in space and time, adaptation of nut-bearing trees to scatterhoarding can only be diffuse. I propose that maintaining variation in seed size may increase the likelihood that seeds are suitable for dispersal by any scatterhoarding species.

The scatter diagrams of dispersal distance as a function of seed size showed an envelope effect, contrary to the expectations of existing cache spacing models. I propose the alternative explanation that the patterns result from differences in the quality of cache sites that animals use for caching different-sized seeds. I present some results from artificial caching experiments suggesting that cache quality differs between substrate type, loose substrates being most concealing and easiest to dig in. This may also explain why the rodents cache many seeds along logs and in palm cones where such substrates are frequently found.

My findings suggest that nut-bearing trees can maximise scatterhoarding and minimise seed predation by producing large crops simultaneously with other nut-bearing trees in the population, but at the same time, they must produce pretty big seeds to maximise the chance of scatterhoarding rather than instant consumption. I evaluate how trees can do so within the limits to their reproductive effort due to nutritional and physical constraints, and conclude that mast seeding, the production of large synchronous crops in alternation with several small crops, is the perfect solution. Rather than trading off seed size and seed number within crops, mast-seeding trees trade-off resources between consecutive crops, displaying large and large-seeded crops in some years at the cost of crops in other years.

Samenvatting

Dit proefschrift gaat over de verspreiding en predatie van grote zaden door hamsterende dieren. Zaadverspreiding zorgt ervoor dat zaden de directe omgeving van de ouderplant verlaten en mogelijk nieuwe plekken kunnen koloniseren. Zaadpredatie daarentegen is het doden van zaden door dieren die ze opeten. Het type hamsteren waarop dit proefschrift betrekking heeft is het verstoppen van zaden op talloze plekken, her en der, met zaadverspreiding als resultaat. Het doel van dit gedrag is het creëren van voedselreserves waarvan die dieren leven in periodes van voedselschaarste, zoals de winter in gematigde streken en het droge seizoen in veel tropische bossen.

Ik onderzocht het hamsteren van nootdragende boomsoorten door grote, cavia-achtige knaagdieren in het ongestoorde tropische regenbos van Nouragues in Frans Guyana, Zuid-Amerika. Deze knaagdieren, agoutis en acouchies, verstoppen zaden een voor een, in ondiepe kuiltjes, elk met een enkel zaad. Door het hamsteren komen zaden weg van hun ouderboom, raken ze geisoleerd van zaden van dezelfde soort, worden ze beschermd tegen zaadetende insecten en gewervelde dieren, en worden ze geplant in de bodem. Deze behandeling is in potentie gunstig voor de kans dat zaden overleven en zich vestigen als zaailing, maar alleen als het dier dat de zaden verstopt ze om een of andere reden niet opgraaft om op te eten. De grote vraag is of de zaadverspreiding door hamsterende dieren opweegt tegen de zaadpredatie, en hoe deze balans wordt beïnvloed door eigenschappen van de plant, zoals zaadgrootte, het aantal geproduceerde zaden, en de fenologie.

Mijn onderzoek legde een verbinding tussen zaadproductie en de vestiging van zaailingen - succesvolle zaadverspreiding - door het individueel volgen van duizenden zaden gedurende het verspreidingsproces. Met videocamera's registreerde ik welke dieren de individueel genummerde en met draadjes gemerkte zaden weghaalden van uitgelegde cafetaria plots. Daarna volgde ik de zaden om te zien wat er met ze gebeurde, daarbij geholpen door uit de grond stekende draden die verrieden waar zaden verstopt lagen. Ik varieerde de zaadgrootte (maar niet de zaadsoort) binnen de cafetaria plots, en deed dat in opeenvolgende jaren die sterk verschilden in de hoeveelheid zaden die in het bos voorhanden was. Zo kon ik zien hoe het hamsteren werd beïnvloed door zaadgrootte en -beschikbaarheid.

Mijn onderzoek had drie doelen. Het eerste was te bepalen of hamsteren een effectief zaadverspreidingsmechanisme was, werkelijk resulterend in gevestigde zaailingen. Dat is nodig om de twijfels weg te nemen over de rol van hamsterende knaagdieren in het bosecosysteem. Het idee dat deze dieren zaadverspreiders zijn leunde tot nu toe sterk op indirecte bewijsvoering.

Het tweede doel was te bepalen of nootdragende boomsoorten afhankelijk zijn van hamsterende dieren voor hun regeneratie. Zo kunnen we te weten komen of de verjonging van deze boomsoorten gevaar loopt in beheerde bossen waar de fauna niet wordt beschermd. Het derde doel was te bepalen hoe zaadgrootte en zaadhoeveelheid de effectiviteit van hamsteren als zaadverspreidingsmechanisme beïnvloeden. Ik wilde toetsen of foerageergedrag en voedselvoorkeur van hamsterende dieren verantwoordelijk kunnen zijn voor de evolutie van grote zaden en het fenomeen van mast bij nootdragende boomsoorten.

Na een algemene inleiding (HOOFDSTUK 1) begint dit proefschrift met een literatuurstudie over zaadverspreiding in tropisch regenbos en over de mogelijke effecten van houtkap op verspreidingssucces en, uiteindelijk, op natuurlijke regeneratie (HOOFDSTUK 2). Aan de hand van literatuur wordt geconststeerd dat er nauwelijks iets bekend is over de gevoeligheid van natuurlijke verjonging voor kwalitatieve en kwantitatieve verandering van zaadverspreiding door dieren. Houtkap en ongecontroleerde jacht die plaatsvindt vanaf de voor houtafvoer aangelegde wegen kunnen negatieve gevolgen hebben voor de verjonging van dierverspreide plantensoorten, en daarmee ook voor veel commercieel interessante boomsoorten. Daarom zou, gegeven de huidige kennis, effectieve bescherming van zaadverspreiders een vast onderdeel moeten zijn van duurzame bosbeheersystemen.

HOOFDSTUK 3 introduceert het verspreidingssysteem dat in dit proefschrift centraal staat – zaadverspreiding door hamsterende dieren – middels een literatuurstudie. De meeste voorbeelden komen van drie nootdragende boomsoorten uit het regenbos van Frans Guyana. Het hoofdstuk legt uit wat verspreid hamsteren is, waarom het belangrijk is voor dieren, en waarom er gedacht wordt dat het eveneens belangrijk is voor bepaalde plantensoorten, in het bijzonder grootzadige bomen. Het hoofdstuk presenteert de huidige stand van kennis, en geeft aan waar de lacunes liggen en welke hypothesen nog moeten worden getoetst.

De volgende hoofdstukken zijn gewijd aan het toetsen van enkele van de plantgecentreerde hypothesen uit HOOFDSTUK 3, gebruikmakend van één van de drie boomsoorten: *Carapa procera*. De zaden van deze soort zijn erg gewild bij hamsterende knaagdieren. HOOFDSTUK 4 stelt de vraag waarom hamsterende dieren überhaupt geïnteresseerd zijn in het verstoppen van deze zaden. Immers, de snelle kieming die karakteristiek is voor *Carapa* zaden verbruikt alle zaadreserves ruim voordat de dieren ze nodig hebben. Uit een serie experimenten blijkt dat de knaagdieren de kieming afbreken door het embryo van de zaden te verwijderen. Zo ontstaan 'zombies' die voldoende lang houdbaar zijn om te kunnen dienen als voedsel in het droge seizoen. De knaagdieren Zo veranderen zo bederfelijke zaden in betrouwbaar voedsel voor de lange termijn.

De HOOFDSTUKKEN 5 TOT 7 presenteren resultaten van de zaadverspreidingsexperimenten waarbij ik videocamera's en draadmerken gebruikte om *Carapa procera* noten in ruimte en tijd te kunnen volgen. Alledrie gaan ze over de consequenties van voedselvoorkeur van de knaagdieren voor zaadpredatie, zaadverspreiding en uiteindelijk de vestiging van zaailingen. Plantensoorten die voor verspreiding afhankelijk zijn van hamsterende dieren hebben verhoudingsgewijs grote zaden. Een intrigerende hypothese die dit verklaart stelt dat grootzadigheid is geëvolueerd als resultaat van selectiviteit van hamsterende dieren die bij voorkeur grote zaden gebruiken voor hun voedselvoorraden. HOOFDSTUK 5 toets de belangrijkste aanname achter dat idee: het hamstergedrag van knaagdieren bevoordeelt grote zaden boven kleinere. Ik onderzocht wat er gebeurde met zaden die sterk uiteenliepen qua gewicht maar wel van dezelfde soort waren. De kans om een zaailing te vestigen was verwaarloosbaar voor kleine zaden in vergelijking met grotere. Dit suggereert dat hamsteren inderdaad selectie naar grotere zaden kan veroorzaken, en betekent dat het gevestigde idee dat het verspreidingsvermogen en de levenskracht van zaden altijd ten koste van elkaar gaan niet geldt voor nootdragende boomsoorten.

Het verspreidingspatroon van verstopte zaden werd ook sterk beïnvloed door zaadgrootte, maar niet op de manier zoals voorspeld door bestaande theorieën. Uit kwantielregressie analyse bleek dat niet alleen de gemiddelde verspreidingsafstand toenam met zaadgrootte, maar vooral ook de reikwijdte van de verspreiding. De resultaten lieten tenslotte zien dat sommige gehamsterde zaden inderdaad overleefden en een zaailing vestigden, ondanks het feit dat het experiment plaatsvond onder voedselschaarste.

Een spectaculair fenomeen dat wordt gedeeld door veel plantensoorten met zaadverspreiding door hamsterende dieren is mast. Jaren met weinig of geen zaadproductie worden afgewisseld met jaren waarin alle individuen tegelijkertijd grote hoeveelheden zaad produceren. HOOFDSTUK 6 toetst een van de oudste en meest bekende functionele verklaringen voor mast, die van het 'overspoelen' van natuurlijke vijanden. Het idee is dat massale zaadproductie in mastjaren zaadpredatoren overstelpt met voedsel, meer dan ze ooit kunnen opeten, zodat veel zaden aan vraat kunnen ontkomen, terwijl tussenliggende jaren met weinig zaden voorkomen dat de zaadpredatoren een overeenkomstig hoog populatieniveau bereiken. Ik maakte een vergelijking van de snelheid waarmee zaden werden gehamsterd en de snelheid waarmee verstopte zaden werden geëxploiteerd tussen drie jaren met veel voedsel en twee jaren met weinig. Ook toetste ik de hypothese - opgeworpen in HOOFDSTUK 5 - dat zaadgewicht in rijke jaren meer invloed heeft op zaadverspreiding dan in magere. De resultaten laten zien dat het reproductief succes in rijke jaren inderdaad veel hoger is, ondanks het feit dat het hamsteren dan in een veel lager tempo verloopt, en dat grotere zaden in rijke jaren nog sterker worden bevoordeeld dan in magere. Grote zaden die temidden van overvloed worden geproduceerd hebben de grootste kans op succesvolle verspreiding en het vestigen van een zaailing.

De twee voorgaande hoofdstukken toetsten het idee dat het hamstergedrag van knaagdieren grote zaden bevoordeelde. Redenerend dat er een zaadgrootte of -gewicht moét zijn waarboven knaagdieren de zaden eenvoudigweg niet meer kunnen dragen, onderzoekt HOOFDSTUK 7 of er een optimale zaadgrootte is voor verspreiding door hamsterende dieren. De resultaten laten zien dat acouchies inderdaad de meest gunstige behandeling gaven aan middelgrote zaden in plaats van aan grootste of kleinste beschikbare zaden. Hamsterende dieren lijken stabiliserende selectie op zaadgrootte te veroorzaken in plaats van gerichte selectie naar almaar grotere (of kleinere) zaden, zoals tot nu toe werd gedacht.

HOOFDSTUK 8 onderzoekt het resultaat van zaadverspreiding, het ruimtelijke patroon van succesvolle, gevestigde zaailingen. Hierbij vergelijk ik drie notendragende boomsoorten, geïntroduceerd in HOOFDSTUK 3, die verschillen in de mate waarin ze worden gehamsterd. Ik vergelijk de verspreiding van zaden, jonge zaailingen en oude zaailingen ten opzichte van ouderbomen en open plekken, om drie ideeën te toetsen. Het eerste – de zogenaamde ontsnappingshypothese – stelt dat zaden en zaailingen in de nabijheid van ouderbomen lijden onder disproportionele sterfte. Alleen de slechtst verspreide boomsoort liet het voorspelde patroon zien. Zaadverspreiding bij de twee andere soorten leek effectief in het vermijden van dergelijke (dichtheidsafhankelijke) sterfte.

Het tweede – de kolonisatiehypothese – stelt dat zaden en zaailingen in de nabijheid van open plekken disproportioneel hogere overlevingskansen hebben. Dit effect was bij geen van de soorten zichtbaar, waarschijnlijk omdat de grote zaden overleving onder sterk beschaduwde omstandigheden mogelijk maken. Dat geen van de soorten vooral werd gevonden in open plekken is waarschijnlijk het gevolg van het mijden van dergelijke geëxponeerde plekken door de knaagdieren.

Het derde idee – dat de beschikbaarheid van licht belangrijker is voor de overleving van zaailingen dan de afstand tot ouderbomen – voorspelt dat zaailingen zich zelfs pal onder ouderbomen kunnen vestigen mits er maar voldoende licht beschikbaar is om te kunnen compenseren voor de verliezen van reserves aan zaadetende insecten. Deze voorspelling werd bevestigd voor *Carapa*. Ik concludeer dat hamsteren voor zaden een effectieve manier is om te ontkomen aan sterfte die is gerelateerd aan de nabijheid van soortgenoten, maar niet om bestaande open plekken te bereiken. Wel vergroten het uitspreiden van de zaden en het uithoudingsvermogen van grootzadige zaailingen in diepe schaduw de kans dat er een zaailing staat waar en wanneer ook een nieuwe plek ontstaat.

HOOFDSTUK 9 is een synthese van alle bevindingen, inclusief enkele resultaten van experimenten die niet in een afzonderlijk hoofdstuk zijn beschreven. De conclusie luidt dat hamsteren een effectief zaadverspreidingsmechanisme is voor nootdragende plantensoorten, en dat het aanzienlijke aantallen gevestigde zaailingen kan opleveren (VRAAG 1). Ook concludeer ik dat *C. procera* afhankelijk is van hamsteren voor het langetermijn voortbestaan in het bosecosysteem. Echter, de natuurlijke verjonging in beheerde bossen lijkt niet onmiddellijk gevaar te lopen indien hamsterende knaagdieren schaars worden, vooral omdat de grotere beschikbaarheid van lichte plekken in het bos de overleving van zaden en zaailingen zal bevorderen (VRAAG 2).

De kans om verspreid te worden én de kwaliteit van zaadverspreiding door hamsterende knaagdieren neemt toe met zaadgrootte, tótdat een grootte wordt bereikt waarbij zaden moeilijker hanteerbaar worden, resulterend in een optimale zaadgrootte voor verspreiding door elke hamsterende diersoort (VRAAG 3). De optimale grootte en de verzameling zaadgrootten die geschikt zijn om te worden gehamsterd zijn waarschijnlijk dierspecifiek en afhankelijk van lichaams- en mondomvang. Omdat nootdragende plantensoorten in ruimte en tijd met verschillende soorten hamsterende dieren te maken hebben, kan de aanpassing van bomen aan hamsteren alleen diffuus zijn. Het behouden van variatie in zaadgrootte kan de kans vergroten dat bomen zaden produceren die geschikt zijn voor verspreiding door verschillende hamsterende diersoorten.

De puntenwolken waarin de verspreidingsafstand was uitgezet tegen zaadgrootte lieten een zogenaamd envelop-effect zien, dat niet strookte met de verwachtingen op basis van bestaande modellen voor verspreid hamsteren. Ik kom met de alternatieve verklaring dat de gevonden patronen voortkomen uit verschillen in de kwaliteit van plekken die dieren gebruiken voor het verstoppen van zaden van verschillende voedingswaarde. De resultaten van experimenten waarin zaden kunstmatig werden verstopt, op allerlei verschillende manieren, suggereren dat de kwaliteit van plekken vooral wordt bepaald door het substraat: los materiaal, zoals vermolmd hout, is het meest verhullend en het makkelijkst om in te graven. Dit is tevens een alternatieve verklaring voor het feit dat de knaagdieren relatief veel zaden verstoppen langs liggende boomstammen en in de bladkegels onder palmen, waar los substraat voorhanden is.

Mijn bevindingen suggereren dat nootdragende bomen hamsteren kunnen maximaliseren en zaadpredatie kunnen minimaliseren door grote hoeveelheden zaden te produceren, gelijktijdig met andere nootdragende boomsoorten in de populatie. Tegelijkertijd echter moeten de geproduceerde zaden ook groot zijn om de kans op effectief hamsteren te vergroten. Ik ga na hoe bomen beide kunnen doen binnen de grenzen van hun reproductieve vermogen, gegeven beperkte hulpbronnen, en concludeer dat mast - het produceren van grote synchrone hoeveelheden zaden in afwisseling met enkele kleine hoeveelheden - de perfecte oplossing is. In plaats van zaadgrootte en de hoeveelheid zaden binnen jaren tegen elkaar af te wegen, ruilen mastende soorten de hulpbronnen van het ene jaar uit tegen die van andere, en produceren ze grote hoeveelheden grote zaden in het ene jaar ten koste van de productie in andere jaren.

Dormitories at Nouragues Biological Station in French Guiana. Photo by Gerrie Offerman

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The author. Photo by Guy Ackermans.

Curriculum vitae

Patricius Alexander (Patrick) Jansen werd geboren in Hilversum op 4 september 1967. Zijn belangstelling voor de natuur was al vroeg zichtbaar, en kwam tot volle bloei toen hij in 1981 lid werd van de Nederlandse Jeugdbond voor Natuurstudie (N.J.N.). Daar hield hij zich gedurende tien jaar bezig met het bestuderen van vogels, loopkevers en zweefvliegen, met natuur- en landschapsbeheer, en met de organisatie van activiteiten. Het ultieme verslag van de inspanningen – de zweeflvliegenatlas van 't Gooi – is nooit verschenen, wat nog altijd op zijn schouders drukt.

In 1985 behaalde hij zijn Atheneum diploma aan het Christelijk College Stad en Lande in Huizen. Na een jaar HBO milieukunde bij de Rijksacademie Nieuw Rollecaete in Deventer, begon hij in 1986 zijn studie biologie aan de toenmalige Landbouwuniversiteit in Wageningen. In dat kader deed hij onderzoek aan het verspreidingsgedrag van loopkevers op de Veluwe, het voorkomen van gespecialiseerde loopkevers op grindbanken langs de Geul in Zuid-Limburg, en de verspreiding van zaden door vogels en apen in het kronendak van tropisch regenbos in Frans Guyana. Daarnaast was hij niet alleen actief bij de N.J.N., maar ook voor de Wageningse jongerenvereniging Unitas en voor de Wageningse studentenwijk Droevendaal. Hij studeerde af in 1993, waarna hij werkte als adviseur voor diverse ingenieursbureaus, als onderwijsassistent voor Wageningen Universiteit, en als docent faunabeheer voor de Leidse Onderwijsinstellingen.

De wetenschap bleef trekken, en in 1995 kreeg hij gelegenheid om bij de vakgroep Bosbouw van Wageningen Universiteit als gastmedewerker van Frans Bongers onderzoekvoorstellen te schrijven en een pilot-onderzoek uit te voeren in Frans Guyana. Zijn subsidieaanvraag voor een vijfjarig onderzoek naar zaadverspreiding door hamsterende knaagdieren in tropisch regenbos werd in 1996 gehonoreerd door de Nederlandse Organisatie voor Wetenschappelijk Onderzoek, en leidde tot dit proefschrift. Gedurende zijn promotie-onderzoek was hij tevens 'burgemeester' van Droevendaal (1995-1998), lid en mede-oprichter van de projectmedewerker-fractie 'PromoV' in de Ondernemingsraad van Wageningen Universiteit (1997-1999), lid van de Raad van Commissarissen van de Stichting Sociale Huisvesting Wageningen (1999-2001), en lid van Provinciale Staten van Gelderland (1999-2003). Bovendien werd hij vader van twee zoons, Simon en Nico.

Sinds 2002 werkt hij als beleidsmedewerker bij de directie Natuurbeheer van het Ministerie van Landbouw, Natuurbeheer en Visserij in Den Haag aan de realisatie van een samenhangend netwerk van natuurgebieden in Nederland, de Ecologische Hoofdstructuur.

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