

22 Observing Seed Removal: Remote Video Monitoring of Seed Selection, Predation and Dispersal

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Introduction

What happens to seeds once they have reached a surface – here referred to as post-dispersal seed fate (cf. Chambers and MacMahon, 1994) – is becoming an increasingly important question. A large body of literature is available evaluating post-dispersal seed fate (reviewed in Hulme, 1998, 2002; Crawley, 2000; Moles and Westoby, 2003; see Hulme and Kollmann, Chapter 2, this volume; Vander Wall and Longland, Chapter 18, this volume). Many studies investigating post-dispersal seed fate, however, measure only seed removal from experimental plots, and implicitly or explicitly assume that removed seeds were killed by seedeaters (see Hulme and Kollmann, Chapter 2, this volume; Forget and Wenny, Chapter 23, this volume; Wenny, Chapter 21, this volume). This approach may be inadequate, as several recent studies in which removed seeds were tracked have shown that many of these seeds are secondarily dispersed rather than consumed (e.g. Vander Wall, 1992, 1997; Forget, 1993; Levey and Byrne, 1993; Brewer and Rejmanek, 1999; Hoshizaki *et al.*, 1999; Jansen *et al.*, 2002). Scatterhoarding animals eat some of the seeds they

gather but bury most seeds as food reserves in scattered caches in the soil (e.g. Jansen *et al.*, 2002; Jansen *et al.*, 2004).

Scatterhoarding may enhance seed survival and seedling establishment because it moves seeds away from the parent and siblings, secures seeds from seed predators such as insects and wild pigs, and puts seeds in situations that often enhance germination and establishment (Vander Wall, 1990). Cached seeds can only establish seedlings, however, if animals leave some proportion of their food reserves untouched. Several studies of secondary dispersal (e.g. Vander Wall, 1994; Jansen, 2003) have shown that scatterhoarded seeds may indeed escape consumption and develop into seedlings. Thus, seed survival and seedling establishment can occur not only right after primary dispersal, but also after one or more subsequent bouts of secondary dispersal (Price and Jenkins, 1986). Moreover, some studies of large-seeded species have observed seeds dying from desiccation or seed predation if they were not removed and buried by scatterhoarding animals (Shaw, 1968; Jansen *et al.*, 2004). Hence, traditional studies of post-dispersal seed survival that simply measure seed removal are insufficient for estimating seed mortality (see

Hulme and Kollmann, Chapter 2, this volume; Wenny, Chapter 21, this volume).

An important aspect of studying post-removal seed fate is finding out which animal species are responsible for seed removal and how they treat seeds. Most studies rely on circumstantial evidence for inferences on agents of seed removal, such as foot prints, observations or captures near experimental seed plots, dental traces on seeds and caching profiles. However, there are several techniques by which actors of seed removal can be identified with greater accuracy and certainty. The simplest are direct observations. Forget (1990), for example, observed from a hide to record removal of *Voucapoua americana* seeds from an experimental plot in French Guiana. He observed that all seeds were removed by a single red acouchy (*Myoprocta exilis*), and he later retrieved most of these seeds in soil surface caches. A technique that allows for monitoring seed removal during longer time spans and at numerous locations simultaneously uses remote cameras (Kucera and Barrett, 1993), in which an infrared sensor detects movement by warm-bodied animals and triggers a camera. Remote cameras have been used successfully to identify terrestrial animals in several studies on terrestrial seed or fruit removal (Miura *et al.*, 1997; Yasuda *et al.*, 2000; Page *et al.*, 2001; Takada *et al.*, 2001; Beck and Terborgh, 2002).

The aim of this chapter is to demonstrate the potential of a third technique, automated remote video monitoring (e.g. Hughes and Shorrocks, 1998), for studying seed removal and seed fate. To do so, we test the following hypotheses using data collected with this technique on animal behaviour and seed removal in large-seeded tree species:

1. Most seed removal is by scatterhoarding animals;
2. Scatterhoarding animals detect seeds more rapidly than do non-dispersing animals;
3. Scatterhoarding animals adapt their foraging activity rhythm to seed abundance;
4. Bigger, more nutritious seeds are removed faster than smaller ones;
5. Bigger, more nutritious seeds are more likely to be scatterhoarded than smaller ones;
6. Higher removal rates are correlated with higher rates of scatterhoarding rather than immediate seed predation;
7. Seed handling time is proportional to the effort scatterhoarders spend on caching, and correlated with dispersal distance;
8. Larger-bodied scatterhoarders disperse large seeds further than do smaller-bodied scatterhoarders.

Note that these hypotheses and tests serve to examine the utility of remote video monitoring rather than as presentations of experimental results.

Sites and Equipment

Most of the data presented in this chapter were collected in 1996–2000 at the Nouragues Biological Station, French Guiana (4°02'N, 52°42'W), an undisturbed tropical lowland rainforest site with an intact fauna (see Bongers *et al.*, 2001, for an extensive description of the site). Terrestrial granivores common in this area include two scatterhoarding rodents: red acouchy (*Myoprocta acouchy*) and red-rumped agouti (*Dasyprocta leporina*). These are important seed dispersers that harvest and cache seeds during the wet fruiting season for use during the lean dry season (Forget, 1990, 1996; Jansen and Forget, 2001; Jansen *et al.*, 2002). Other rodent species in the area, i.e. Guianan red squirrel (*Sciurus aestuans*), Cuvier's terrestrial spiny rat (*Proechimys cuvieri*), bristle mouse (*Neacomys guianae*) and rice rat (*Oryzomys megacephalus*), are primarily seed predators (Guillotin, 1982; Guillotin *et al.*, 1994; Henry, 1997). Species in these genera may hoard seeds, but probably put most seeds in places that are unfavourable for seedling establishment, such as in larders, burrows or up in trees (Forget, 1993; Brewer and Rejmanek, 1999; P.A. Jansen, Nouragues, 1998, personal observation). White-lipped peccary (*Tajassu pecari*) and collared peccary (*T. tajacu*) are potential dispersers of small

seeds (see Hulme and Kollmann, Chapter 2, this volume; Wenny, Chapter 21, this volume), but they destroy most of the large seeds they ingest (Kiltie, 1981, 1982; Bodmer, 1991; see Beck, Chapter 6, this volume). The ecological role of the two *Mazama* deer species in the area (see Gayot *et al.* 2004), finally, is probably comparable to that of peccaries. With the exception of rats and mice, all species are (primarily) diurnal at Nouragues.

In addition, we collected data in 1998 at Speulderbos, a mixed oak–beech forest in The Netherlands (52°15'N, 5°40'E; see den Ouden, 2000, for further site description). Terrestrial granivores in this area include two rodent species, bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*), and two ungulates, Eurasian wild boar (*Sus scrofa scrofa*) and red deer (*Cervus elaphus*). Here, wood mice are the only mammals that scatterhoard seeds (see den Ouden *et al.*, Chapter 13, this volume).

At Nouragues, we established over 250 experimental plots with more than 6500 seeds in the understorey throughout the area. Each plot measured 0.5 to 1.0 m² where we removed litter and placed 9, 25, 49 or occasionally 100 fresh seeds. We arranged seeds in regular grids in order to identify them individually by their position. Overall, we used a dozen different seed species, but most plots contained seeds of either *Carapa procera* (Meliaceae; $n = 109$ plots, 3500 seeds) or *Licania alba* (Chrysobalanaceae; $n = 59$ plots, 1300 seeds), two large-seeded tree species (henceforth *Carapa* and *Licania*). These seeds were weighed, thread-marked and individually numbered. Marking enabled retrieval and identification of seeds after removal, as the thread and tag protrude from the soil even when seeds are cached (Forget, 1990; see Forget and Wenny, Chapter 23, this volume). Our experimental period included 3 years of abundant fruiting (1996, 1998 and 2000) and 2 lean years (1997 and 1999). At Speulderbos, we established five experimental seed plots, each including 49 acorns of *Quercus robur* (Fagaceae) arranged in a 7 × 7 grid. At Speulderbos and in most experiments at Nouragues, we manipulated seed fresh mass within

seed plots to study size-discrimination by scatterhoarding rodents: each plot included as wide a range of (intraspecific) seed masses as possible (cf., Jansen *et al.*, 2002; Jansen *et al.*, 2004).

We monitored animal activity and seed removal by remote video recording at plots for several hours up to several days, depending on the seed removal rate. Then, from the playback, we recorded the identity of animals and the time of removal for each individual seed, as well as some behavioural observations. Our equipment consisted of a monochrome CCD video surveillance camera (Philips VCM 6250/00T) in a weatherproof housing (Eneo VHL-2EC) and a time lapse video recorder (Panasonic AG-1070 DC). Power came from 12V 18Ah car batteries that we replaced daily and recharged at the field lab using solar panels. Much smaller, more energy-efficient and more advanced systems are now available (see Discussion). The camera was mounted on a tree next to the plot at ~ 1.5 m height using an aluminium wall bracket (Eneo WD-14/MK). The recorder was attached to a tree 2–3 m away from the plot, in a waterproof bag with silicagel. Depending on ambient humidity, video recording was either triggered by a passive infrared detector (ASIM IR 207, not waterproof enough for rainforest conditions) or continuous in time-lapse mode (four frames per second). Recordings were on ordinary VHS tapes, on which date and time in seconds were also visible. At Speulderbos, we only recorded seed removal over night, using an infrared (IR) lamp (Dennard 880M20 microlight). In Nouragues, in contrast, nocturnal seed removal in a first series of trials with this IR lamp was so rare that we decided to use all power for recording diurnal animal activity and seed removal.

Results

The most basic purpose of video monitoring seed removal is to identify the animal species that visit seed sources and remove seeds. At our seed plots in Nouragues, we

recorded a suite of different animals, including most of the ungulate and terrestrial rodent species occurring in the study area, and many other terrestrial animals. The recordings allowed separating animals that actually took seeds from those that did not. The only animals taking seeds by day in Nouragues were red acouchy, red-rumped agouti, collared peccary (Fig. 22.1A–C, respectively) and Guianan red squirrel. Most, but not all, visits by these species resulted in seed removal (here including *in situ* consumption of seeds). If we had inventoried seed removers by occurrence of foot prints, a frequently used method in studies of seed removal, we would have produced a longer, less accurate list of potential seed dispersers and predators. Likewise, we found that only wood mice removed acorns from our seed plots at Speulderbos, whereas live rodent trapping prior to the experiments had shown that bank voles were more common than wood mice.

Discovery of seeds

More beneficial to plants than simply removing seeds is that scatterhoarders remove seeds before non-dispersing animals get a chance to find them. We studied how much time it took different granivorous mammals to discover the artificial seed sources in Nouragues, using the time indication on our video recordings. We measured the time until discovery for each animal species at 102 plots, and compared the rates using Kaplan Meier survival analysis. Times were right-censored at the end of our recordings if a species was not seen visiting a plot within the video observation period. We found that the two scatterhoarding rodents detected plots significantly more rapidly than did the other granivores (log-rank test: $\chi^2_1 = 111$, $P < 0.001$; Fig. 22.2A). Acouchies were the first to discover seed plots in 96% of the cases, and were always earlier than agoutis. Their higher abundance and smaller home range compared to agoutis and peccaries (Dubost,



Fig. 22.1. Video stills of granivorous mammals, viewed from above, visiting cafeteria plots with different-sized *Carapa procera* seeds in a French Guianan rainforest. (A) red acouchy (*Myoprocta acouchy*), (B) agouti (*Dasyprocta leporina*) and (C) collared peccary (*Tajassu tajacu*). The time indication (upper left corners) and organization of the seeds in a grid allowed for measurement of time and sequence of removal of individual seeds by different species or even individuals. The black dots visible on photo B are black-painted heads of roofing nails, pressed in the ground below each seed, that appear upon seed removal.

1988) increased the probability of acouchies discovering and rapidly sequestering seeds before larger and stronger competitors could monopolize the food.

An important determinant of the ability of species to obtain seeds is their activity rhythm. In Nouragues, seed removal occurs primarily during the day, and the early morning should therefore be a good time for granivores to monopolize fallen seeds that have accumulated over night. We used our recordings to investigate the foraging activity of different granivores during the day, counted how many seeds each species took for each hour of the day, and calculated rates of seed removal for each species. We did this separately for years of high and low seed abundance to see how food availability influenced activity patterns. We found that the overall foraging activity of acouchies

peaked in the early morning and the late afternoon (Fig. 22.3). Both agoutis and acouchies showed reduced activity at mid-day. This 'siesta' may serve to avoid the high mid-day temperatures as well as the rain showers that frequently occurred around noon, but we also observed that acouchies got increasingly bothered by horseflies and other insects over the course of the morning.

Acouchies showed a strong apparent response to food abundance. As predicted, their morning activity was greater in low seed years than in high seed years, and also continued longer. Peccaries, in contrast, were only recorded around noon and only in low seed years, but this pattern may have been an artefact of the low number of encounters. Discovery times that we recorded for *Carapa* seed plots in years of

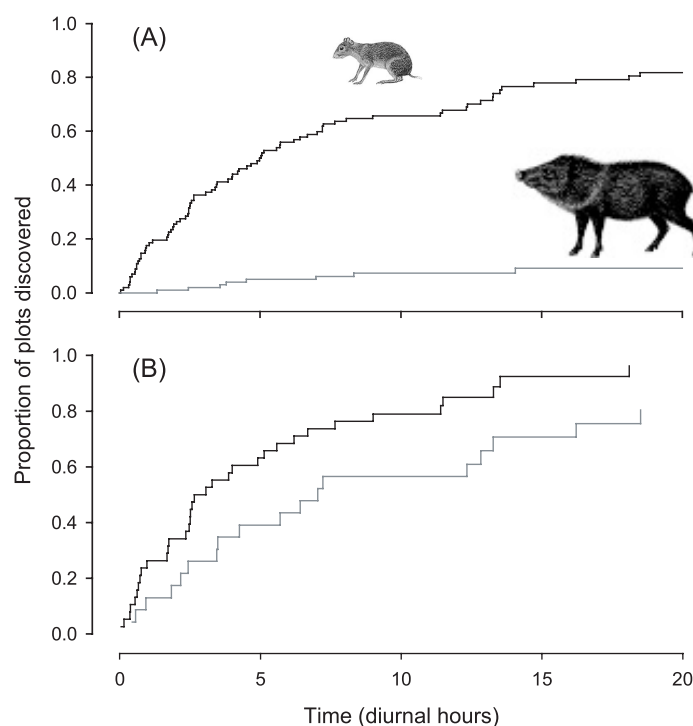


Fig. 22.2. Time to detection of experimental seed plots by granivorous mammals in a French Guianan rainforest, based on video surveillance data. (A) Agoutis and acouchies (upper line) were much more rapid in detecting plots than were non-scatterhoarders such as collared peccaries (lower line). Data are from 102 seed plots ranging in seed species, size, site and date. Seeds were at least 1 g fresh mass and included monkey-dispersed species, bird-dispersed species, and nut-bearing species. (B) Acouchies detected *Carapa procera* seed plots more rapidly in low seed years (upper line) than in high seed years (lower line).

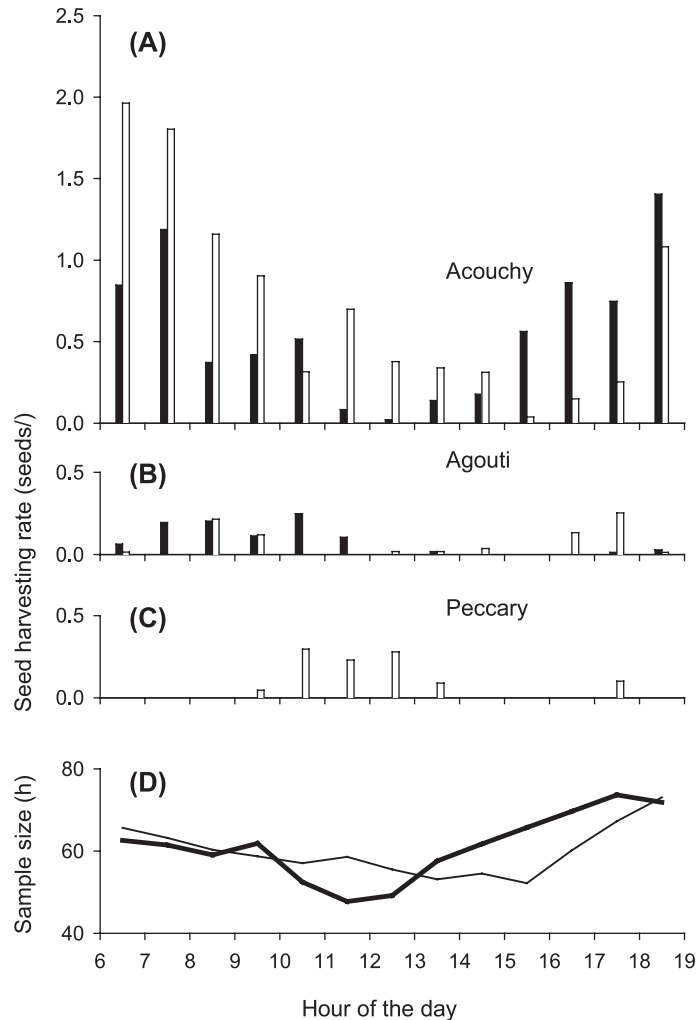


Fig. 22.3. Activity patterns of three granivorous mammals at 152 experimental seed plots in French Guianan rainforest, based on video recordings. Plotted is the average number of seed removed per hour, for different hours of the day, by acouchies (A), agoutis (B) and peccaries (C), respectively. The bottom graph (D) shows the sampling intensity in terms of total hours of video per time interval. White bars and thin lines indicate low seed years, black bars and bold lines represent high seed years. Plots included *Carapa procera* (68) and *Licania alba* (49) or one of ten other species (45 plots). 1670 seed removal events were recorded.

contrasting seed abundance also suggest that acouchies increase foraging activity under food scarcity. Acouchies discovered the plots significantly more rapidly in low seed years (median time 171 min, $n = 38$ plots) than in high seed years (422 min, $n = 23$) (logrank test: $\chi^2_1 = 5.4$, $P = 0.02$; Fig. 22.2B). Food scarcity apparently increased foraging effort, which increases the probability of acouchies finding a given seed source.

Predators or dispersers?

Most plant species have several animal species that potentially eat their seeds, but these animals often differ in their impact on seed fate. Some species ignore the seeds, others act primarily as seed predators that immediately consume the seeds they find, and yet others act as potential seed dispersers by transporting seeds away from

the parent plant and caching them. Members of the latter group, in turn, will differ in their performance as seed dispersers. Determining the impact of animal species therefore requires detailed seed fate data. We compared the contributions of different granivore species as predators and dispersers of two seed species, *Carapa* and *Licania*. Seeds of *Licania* are larger and have a greater nutritional content and longer storage life than *Carapa* (Jansen and Forget, 2001) and thus should be more valuable for storage purposes. We used video monitoring to identify the agent of removal for each individual seed in our experimental plots. We then searched the surrounding area to retrieve removed seeds by their numbered threadmarks and record their fate. This made it possible to link individual seed fates to granivorous species or even individuals, and to assess the contribution of each animal species to predation or dispersal.

Figure 22.4 shows the proportions of seeds removed by four species of granivores for each seed species. Peccaries and squirrels removed few of the seeds (Peccaries removed 5% of *Carapa*, squirrels 2% of *Licania*), yet they accounted for an important part of seed mortality. Peccaries crushed and consumed all *Carapa* seeds they handled, and accounted for 35% of all *Carapa* seeds found eaten. Squirrels take *Licania* seeds into trees and liana tangles (P.A. Jansen, Nouragues 1998, personal observation). Because these sites are unsuitable for seedling establishment, arboreal caching is equivalent to killing seeds even if the seeds are not eaten. Acouchies accounted for the majority of recorded removal in both *Carapa* (62%) and *Licania* (60%). Far most of the removed seeds that we retrieved were scatterhoarded (86% in *Carapa* and 99% in *Licania*). Agoutis, finally, were less important seed removers than acouchies, even though agoutis are especially well-known for scatterhoarding seeds in the Neotropics (e.g. Smythe, 1970; Forget and Milleron, 1991; Forget, 1992, 1993; Hallwachs, 1994; Peres and Baider, 1997; Silvius and Fragoso, 2003). They removed few *Carapa* seeds (2% of removal)

but quite some *Licania* seeds (13%). We retrieved a low proportion of these seeds, and while most of these in *Carapa* were eaten (71%), all *Licania* seeds were scatterhoarded. For acouchy and agouti, removed seeds that we did not find were likely carried beyond the radius of our search area (see below). Hence, the smaller percentage consumed in *Licania* suggests that acouchies stored more seeds of this high-value species, while the smaller proportion of seeds we located suggests that dispersal of this preferred species was also further.

Body size and dispersal distance

Agoutis are two to six times heavier than acouchies (Emmons and Feer, 1997). Hence, we may expect that handling and transporting large nuts is easier for agoutis than for acouchies, and that agoutis disperse a given large seed species further than do acouchies. To test this prediction, we compared plot-to-cache distances of 415 individually thread-marked *Licania* seeds removed by acouchies to 105 seeds removed by agoutis. Contrary to our expectations, we found no significant difference in dispersal distance between agoutis and acouchies (log rank test: $\chi^2_1 = 0.44$, $P = 0.508$; Fig. 22.5), at least not for the first 25 m. This suggests that agoutis and acouchies have a similar impact with regard to dispersal distance, even though they differ in their seed preference.

Seed removal rates

The rate of seed removal varies widely among plant species, animal species, year and habitat. Many published studies treat removal rate as predation rate, with rapid removal treated as equivalent to low post-dispersal seed survival. If, however, the removal rate represents the motivation of animals to sequester and scatterhoard seeds, removal rate might rather be indicative for secondary seed dispersal, with rapid removal by scatterhoarders

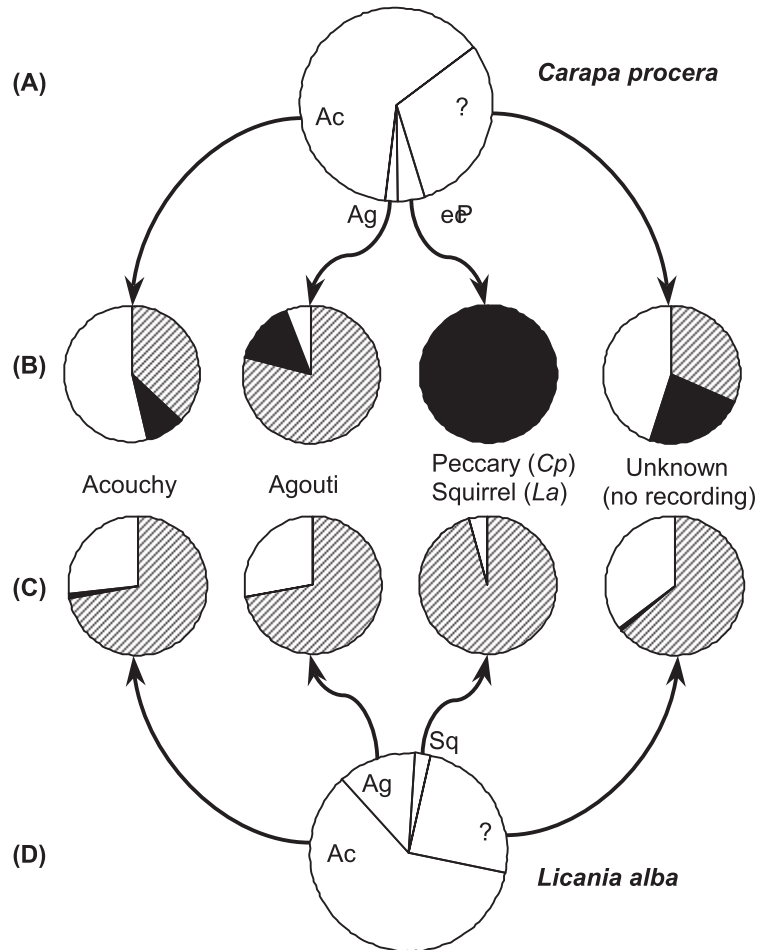


Fig. 22.4. Identities of mammals removing seeds of two large-seeded tree species in French Guianan rainforest, determined from remote video recordings, and the subsequent fate of seeds. (A) Proportions of rapidly germinating *Carapa procera* seeds ($n = 1537$) removed by different granivorous mammal species, and (B) the primary seed fate for each agent, with white slices indicating cached, black eaten, and hatched unknown (not retrieved on soil within the search radius). (D) Proportions of the slowly germinating *Licania alba* seeds ($n = 963$) removed by different granivorous mammal species, and (C) primary seed fate for each agent (slice patterns as in B). Question marks in (A) and (D) indicate the proportion of seed removal for which we had no video recordings. *L. alba* has a much slower germination rate and, thus, longer seed storage life than *C. procera*, and was therefore favoured as food. For acouchy and agouti, many of the missing seeds (B and C) were presumably dispersed beyond the search radius, especially in *L. alba*.

shortening the seed's exposure to seed predators. To investigate whether immediate predation of seeds in Nouragues increased with removal speed, we correlated the proportion of *Carapa* seeds consumed by mammals to the median time-to-removal of individual plots. We used video surveillance to record the exact times that seeds were removed during 1 or a few days. If it

took longer for plots to be depleted, we switched to the standard method of recording seed presence according to a regular scheme of censuses. This approach allowed us to capture subtler differences in removal speed than with the standard method alone. Mean removal times of *Carapa* seed plots in French Guiana ranged from several hours to several weeks (Fig. 22.6). Plots with high

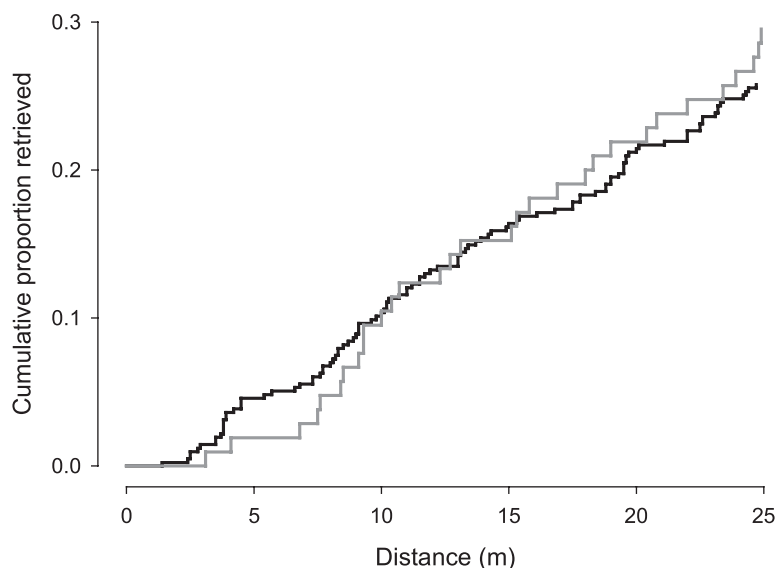


Fig. 22.5. Comparison of dispersal distances between different-sized scatterhoarders in French Guiana. Plotted is the cumulative retrieval of *Licania alba* seed caches made by red acouchies (*Myoprocta acouchy*; black line) and considerably larger red-rumped agoutis (*Dasyprocta leporina*; grey line), as a function of an increasing search radius from seed plots. Remote video recordings of seed removal were used to assign seeds and caches to animal species. Estimated cache distances were not significantly different (see text). Note that less than 30% of the seeds were found cached within 25 m; most of the remaining 70% were assumed to be dispersed beyond that distance, not actually found by us.

removal rate tended to have lower proportions of removed seeds eaten, rather than scatterhoarded, than did plots with slow removal rates (linear regression with time log-transformed: $\beta = 0.124$, $F_{1,43} = 7.9$, $P = 0.007$, $R^2 = 0.16$). Rapid seed removal in Nouragues is also correlated with larger dispersal distances (Jansen *et al.*, 2004). Both rapid removal and greater dispersal distance indicate a higher motivation of rodents to carefully store the seeds. If this pattern holds for other species and habitats, rapid seed removal could be a sign of higher-quality seed dispersal rather than higher predation.

Selectivity

Agoutis and acouchies in French Guiana and wood mice in The Netherlands remove and disperse only one seed at a time. We hypothesized that rodents would give

priority to removing the biggest seeds, because those have the greatest nutritional value, and yield the high reward per caching effort and per cache (Smith and Reichman, 1984). The alternative strategy of removing seeds randomly, regardless of food value, would lengthen the exposure time of high-value seeds, and thus increase the risk of such seeds being monopolized by competitors. To test whether animals discriminated among seed sizes during removal, we determined the order of seed removal from *Carapa* experimental plots in which seed fresh mass varied widely (cf. Jansen *et al.*, 2004). We used video recordings to determine the exact sequence of seed removal. Then, we standardized and lumped the data from all plots, and used least absolute deviation (LAD) regression for different quantiles to test whether heavier seeds were given any priority. The significance values for fitted quantile regressions were calculated from 10,000 permutations (see Jansen *et al.*, 2002, for

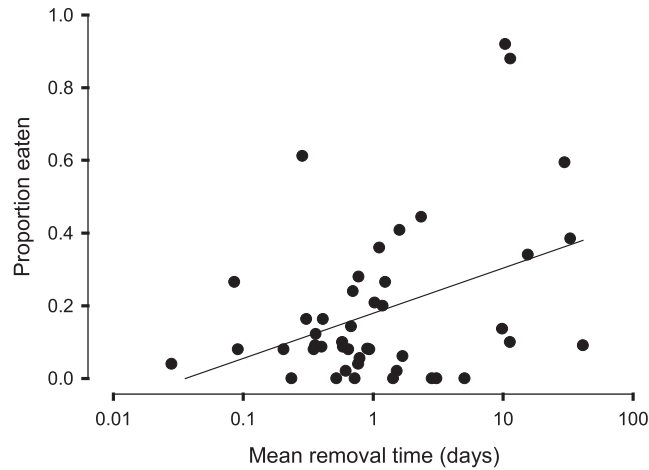


Fig. 22.6. Rate of *Carapa procera* seed removal from experimental plots in French Guiana and the proportion of seeds subsequently found consumed. Rate was calculated as (mean removal time)⁻¹, and mean removal time was estimated as the total waiting time of all seeds divided by the number of seeds removed. Rapid removal was correlated with low rates of immediate seed consumption (see text).

analysis details). There was indeed a tendency for large seeds to be removed before small seeds (Fig. 22.7): regressions at all quantiles had significant negative slopes, although significant only at the quantiles ≥ 0.25 . The coefficient values, however, were modest (average $\beta = -0.003$), indicating that the effect was rather weak. The position of seeds within plots can have a greater effect on seed removal than seed size (Jansen *et al.*, 2002; see den Ouden *et al.*, Chapter 13, this volume).

Seed handling time

Seed fate studies generally suffer from incomplete retrieval of cached seeds (see Forget and Wenny, Chapter 23, this volume). Missing seeds are difficult to account for because they can be either overlooked within the search area, taken into burrows or into trees where they die, or dispersed outside the search area. Not accounting for missing seeds can cause serious bias in dispersal distances and survival rates, but so can assumptions on the fate of such seeds. We therefore investigated whether the handling time could serve as an alternative estimate for dispersal. In our experiments at

Speulderbos, we used video recordings to calculate the exact time that elapsed between the removal of numbered and magnet-tagged acorns by individual wood mice and their return to the plot for removing the next seed. Subsequently, we searched for scatterhoarded seeds with a magnetometer and measured their distance to the experimental plots as well as cache depth. Indeed, the time interval between visits correlated significantly with both plot-to-cache distance (linear regression, time and distance log-transformed: $R^2 = 0.42$, $F_{1,185} = 138$; $P < 0.001$; Fig. 22.8A) and cache depth ($R^2 = 0.10$, $F_{1,185} = 19.4$; $P < 0.001$; Fig. 22.8B), two elements of dispersal positively correlated with seed survival (e.g. Vander Wall, 1993; Hammond and Brown, 1998). The combined model $\log(t) = 1.57 + 0.73 * \log(\text{distance in m}) + 0.37 * \log(\text{depth in cm})$ explained more than half of the variation in interval duration (multiple regression: $R^2 = 0.51$, $F_{2,185} = 96$, $P < 0.001$). Cache distance and depth were not correlated ($r = 0.02$, $P = 0.78$). We conclude that interval time between visits was proportional to the investment of rodents in scatterhoarding and their performance as seed dispersers, and can be used as a potential estimate of dispersal under incomplete seed retrieval.

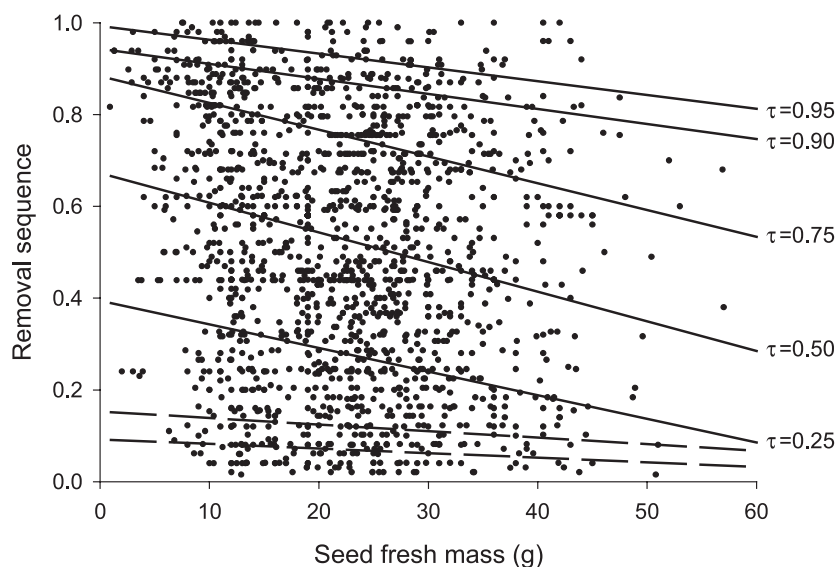


Fig. 22.7. Size-discrimination by granivorous mammals during removal of seeds from cafeteria plots in a French Guianan rainforest. Plotted is the standardized removal sequence for 1638 *Carapa procera* seeds from 44 plots. Seeds that were among the first to be removed from a plot have sequence values near 0, whereas seeds among the last to be removed have values near 1. Lines are least absolute deviation regressions for different quantiles τ . The continuous lines indicate quantile regression slopes that were significantly different from zero ($P < 0.0002$), indicating that large seeds were removed faster than smaller ones. The quantile regressions at $\tau = 0.05$ and 0.10 (broken lines) were not significant ($P > 0.05$). P values were determined from 10,000 permutations.

Discussion

We have demonstrated that remote video monitoring of post-dispersal seed removal makes it possible to address a variety of questions that cannot be answered using traditional field methods. Video recordings allow for distinguishing actual dispersers and predators, and for linking agents to the fate of individual seeds. Both in French Guiana and The Netherlands, we found that most or all seed removal was by a single rodent species which scatterhoarded most or all of the seeds it took. We compared the performance of acouchies and the larger agoutis as seed dispersers and found that they produced indistinguishable seed shadows, at least at shorter distances. Video surveillance can also be used to measure the exact times at which events occur. Time recordings revealed that scatterhoarding rodents discovered seed plots much more rapid than non-scatterhoarding mammals. Acouchies had the highest probability of

encountering seed sources, and were able to further increase this probability by shifting their activity towards the early morning in low seed years.

We have also shown how time recordings are an improvement compared to the standard method of recording seed presence in intervals, because it yields continuous data that can be more effectively analysed using survival analysis (e.g. Fox, 1993; Zens and Peart, 2003), without problems of interval-censoring, and, if necessary, with detection time and removal time separated. The ability to capture subtle differences in removal rate allows for comparisons even if seed removal is rapid (e.g. for preferred seed species or under seed scarcity). Thus, we found that rapid removal of nuts in French Guiana was indicative of high secondary dispersal rather than high immediate predation. Finally, remote video monitoring cannot only provide detailed measurements of seed fate pathways and event histories, but also yields data on the behaviour of

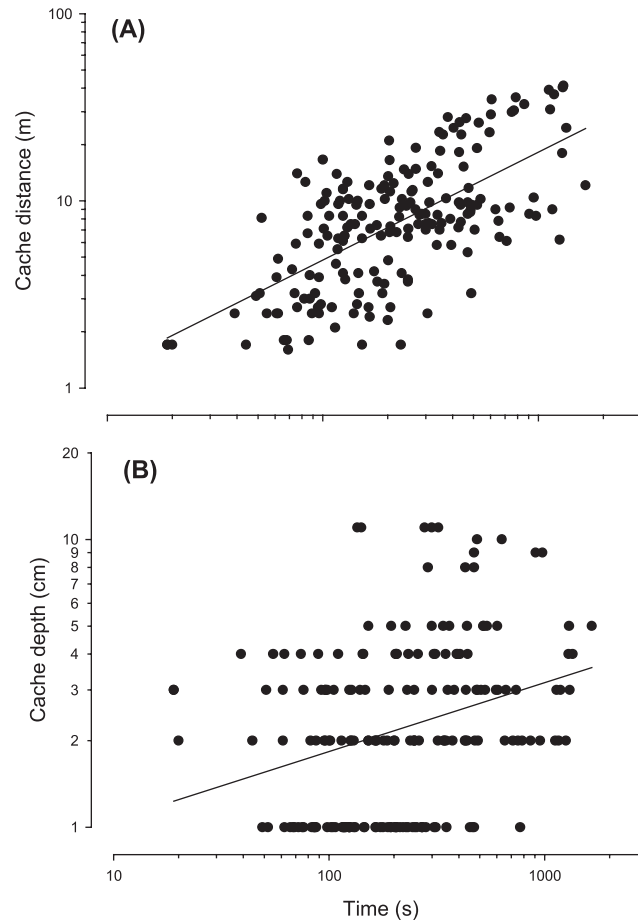


Fig. 22.8. Scatterhoarding of acorns (*Quercus robur*) by wood mice (*Apodemus sylvaticus*) in a Dutch oak–beech (*Fagus sylvatica*) forest. Time elapsed between an individual removing an acorn and that same individual returning for the next acorn was correlated with the subsequent (A) cache distance and (B) cache depth of that same acorn. The interval between subsequent removal events was proportional to caching effort and dispersal distance.

free-ranging animals that discover and explore seed plots. We showed, for example, that granivores in French Guiana tended to remove large seeds before smaller ones, supporting the idea that large seeds are preferred to small ones (Smith and Reichman, 1984). And we showed that time intervals between successive visits of wood mice to seed plots in The Netherlands were proportional to the dispersal distance of scatterhoarded acorns. Interactions between food competitors at seed sources are another example of this type of behavioural data (e.g. den Ouden *et al.*, Chapter 13, this volume).

Remote video monitoring has already been applied in a wide range of animal field

studies, including provisioning rates and predation at bird nests (e.g. Ouchley *et al.*, 1994; Franzreb and Hanula, 1995; Delaney and Grubb, 1999; Keedwell and Sanders, 2002; Stake and Cimprich, 2003), behaviour of badgers (*Meles meles*) at middens (Stewart *et al.*, 1997), activity of overwintering bats in caves (Sedgeley, 2001), predation of reef sponges (Dunlap and Pawlik, 1996) and the use of fauna passages (Mathiasen and Madsen, 2000). Video cameras have even been mounted on the back of seals to study their hunting behaviour (Davis *et al.*, 1999). However, this technology has not been applied to seed fate studies (but see Jansen *et al.*, 2002; Jansen *et al.*, 2004; see den

Ouden *et al.*, Chapter 13, this volume). Complications for use in field studies in the past have been, amongst others, the equipment's bulkiness, sensitivity to weather and high cost.

Recent technological and methodological innovations have made remote monitoring of seed removal in the field increasingly feasible. Compact, high quality systems can now be assembled largely from consumer electronics readily available at reasonable cost. Digital techniques permit computer storage and analysis of video fragments, which can be copied into presentations or other media. Digital video cameras can record at low light levels, and have built-in features for nocturnal recording using an infrared beam to illuminate study areas. Most models can record date and time in seconds. The cameras come with compact lithium batteries that allow for up to 10 or more hours of recording and up to several weeks of standby, and higher-capacity batteries are also available. Waterproof housing, required for operating these cameras outdoors, is available from camera brands as well as specialist diving companies. The typically yellow cases can be painted in camouflage colours and mounted on a tree or post using a wall bracket. Passive infrared sensors allow recording of events only, switching the camera to standby if there is no vertebrate activity. A more up-to-date system that we are now using is a Sony DCR-VTR18E mini DV handycam in Sony® SPK-TRV33 weatherproof housing in combination with a TrailMaster® 700v passive infrared sensor. A good but cheaper alternative for electronic control of digital cameras, 35 mm cameras and video camcorders is PixController® control boards that use an integrated Passive Infrared (PIR) Motion Control circuit to trigger devices.

Monitoring seed removal with remote video cameras is especially efficient if seed removal is rapid. Then, it takes only 1 or few days to record near-complete depletion of a seed plot, after which the camera can readily be used for the next replicate. Realizing ten replicates per month with a single camera unit is then feasible, allowing sufficient replication within a limited time span

(fieldwork period or fruiting season) to capture variation in removal rates and seed fates between sites and individuals with only one or few cameras. However, remote video cameras are less practical for full monitoring of plots with slow seed removal rates, because one would need to operate many parallel systems. In our experiments, we usually stopped video monitoring after 2 or 3 days if seed removal was slow, because we found replication more important. Photo-camera traps are cheaper and seem a more suitable way for monitoring slow seed removal and other relatively rare events simultaneously at many places.

Remote video monitoring cannot replace studies of post-removal seed fate, in which seeds are tracked until they either die or establish seedlings. Without data on the ultimate fate of cached seeds, video recordings still leave plenty of room for the argument that scatterhoarding is only putting off the evil hour – cached seeds are food reserves – and is of negligible net benefit (e.g. Larson and Howe, 1987; Pena-Claros and De Boo, 2002). What video surveillance can do, however, is strongly reinforce seed fate tracking experiments and thereby make such high-effort studies more rewarding.

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