17 Rodent Scatterhoarders as Conditional Mutualists

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Introduction

Seeds dispersed by vertebrates can face potentially very different seed fate pathways. One of these is via vertebrates that pose little threat to the seed itself, either dropping the seed in the course of fruit handling or passing the seed relatively unharmed through the gut ('benign dispersers' or 'legitimate' dispersers of Schupp (1993)). Alternatively, seeds could be dispersed by vertebrates that potentially act as either seed predators or seed dispersers by consuming and damaging a significant proportion of seeds they handle. One set of animals that act in this way are those that ingest seeds and pass them through the gut (Janzen, 1981; see Beck, Chapter 6, this volume). Another set includes animals that temporarily cache seeds for later consumption, and occasionally fail to recover some of these seeds, thereby acting inadvertently as seed dispersers (Vander Wall, 1990). Because of the large cost in seeds destroyed by the latter two groups, and the difficulty in estimating the relative benefits of dispersal by these animals to plant recruitment, whether they play the role of antagonistic seed predator or mutualistic seed disperser is often equivocal (see Hulme, 2002; Beck, Chapter 6, this volume).

Variation in the outcome of species interactions like that exhibited by animals that can potentially destroy or disperse seeds has been documented in several systems that traditionally have been viewed as mutualisms (e.g. ant-membracid mutualisms; Cushman and Whitham, 1989; Billick and Tonkel, 2003). In these systems, termed 'conditional mutualisms', variation in ecological and life-history factors in either space or time can shift the outcome of a species interaction to multiple points along the continuum from antagonistic to mutualistic (Bronstein, 1994).

In this chapter, I argue that the interaction between plants and the rodents that scatterhoard their seeds (i.e. cache seeds individually or in small groups in numerous cache locations) can be viewed as a conditional mutualism that depends in part on two factors that can vary in time and space:

1. The relative abundance of seeds versus scatterhoarders (the seed:scatterhoarder ratio);
2. The potential recruitment of seedlings that are not handled by scatterhoarders versus recruitment when seeds are handled by scatterhoarders.

In a review of conditional mutualisms, Bronstein (1994) argued that variation in the outcome of species interactions was more likely when: (i) the mutualism was facultative rather than obligate; (ii) a third species was intimately involved in the interaction;

Seed Fate
(eds P.-M. Forget, J.E. Lambert, P.E. Hulme and S.B. Vander Wall)

and (iii) the benefit of the interaction was a function of the relative abundance of the partners. All or several of these conditions are met by the scatterhoarder–plant interaction. First, although some scatterhoarder–plant interactions have been argued to be obligate (Hallwachs, 1986; Smythe, 1989; Forget, 1990; Peres *et al.*, 1997; Asquith *et al.*, 1999) many appear to be facultative, with at least some possibility for plant recruitment in the absence of the scatterhoarder. Second, one advantage of dispersal by scatterhoarding in some systems is escape from an independent mortality agent acting on undispersed seeds in the form of other seed predators and pathogens. Third, the number of seeds available relative to scatterhoarder density affects scatterhoarder behaviour, both in the proclivity to cache seeds rather than eat them and in the probability that seeds may survive caching.

In this chapter, I develop a simple conceptual model of how the outcome of the scatterhoarder–plant interaction depends on both the relative abundance of each partner and the challenges to recruitment faced by the plant. I also describe ways in which both factors can be altered by natural and anthropogenic changes that shift the outcome of the interaction, resulting in the type of context-dependent scenarios described by Dennis *et al.* (Chapter 7, this volume). In developing the model, I have considered primarily the interaction between a single scatterhoarder species and a single plant species, independent of the relative effectiveness of one scatterhoarder species to another or to other dispersers (disperser effectiveness *sensu* Herrera and Jordano, 1981; Schupp, 1993), or of how the same scatterhoarder can act as a predator for some plant species and a mutualist of others (e.g. differential caching and handling of red and white oaks by squirrels) (Hadj-Chikh *et al.*, 1996; Steele *et al.*, 2001; Steele *et al.*, Chapter 12, this volume).

Conditionality and the Seed to Scatterhoarder Ratio

Large fruit and seed crops have been argued to be important for satiating seed predators (Janzen, 1971a; Silvertown, 1980) and, when followed by periods of food scarcity, for stimulating seed hoarding behaviour (Smythe, 1970; De Steven and Putz, 1984; Schupp, 1990; Vander Wall, 1990; Sork, 1993; Forget *et al.*, 2001). The effect of seed/fruit abundance on scatterhoarder behaviour has been studied at three levels: (i) the amount of the crop handled by scatterhoarders; (ii) the fate of seeds initially handled (either cached or eaten); and (iii) the probability that cached seeds survive to germinate. In some cases, high seed and fruit availability has been shown to increase the proportion of the crop that escapes handling altogether, but even in years of high seed production entire crops can sometimes be harvested by scatterhoarders. Likewise, large crops have been shown to increase the ratio of seeds cached versus those eaten, though this too is not always true. Finally, although the assumption that increased caching would translate into higher probability of seed survival in caches is intuitive, studies linking seed abundance and cache fate are relatively rare. Vander Wall (2002) demonstrated that although rodent scatterhoarders cached nearly all seeds in years of both high and low pine (*Pinus* spp.) seed crops, fewer seeds were consumed and more caches survived to time of germination in years of large seed crops. Likewise, caches of seeds of the tropical rainforest tree *Beilschmedia bancroftii* made by white-tailed rats lasted significantly longer in a year of heavy seed fall than in years when no seeds were produced (Theimer, 2001). Hoshizaki and Hulme (2002) quantified seed production for three tree species (*Aesculus turbinata*, *Fagus crenata* and *Quercus mongolica*), densities of two rodents (*Apodemus speciosus* and *Eothenomys andersoni*) and seed fate for *Aesculus turbinata* over several years that varied in total seed and rodent abundance. They found that the percentage of seeds initially cached (versus eaten) and moved to secondary caches was highest in a year of greatest seed availability. However, they found no detectable difference in cache survival across years, in part because the number of experimental seeds surviving to germination was very small in all years.

I developed a simple graphical model to describe the hypothetical relationship between survival of undispersed seeds and scatterhoarder cached seeds as a function of seed abundance (Fig. 17.1). Because the relative abundance of scatterhoarding rodents often varies in space and time, crop size alone will not predict seed fate as well as a measure of the relative abundance of seed/fruit availability to scatterhoarders. Therefore, I used the ratio of seeds : scatterhoarders in developing the first stage of this model. Figure 17.1 shows the proportion of a seed crop handled by scatterhoarders approximating 100% at low seed : scatterhoarder ratios and eventually declining as the number of seeds relative to scatterhoarders increases. The proportion of seeds that escape handling by scatterhoarders would obviously be the inverse function. The proportion of the crop that potentially survives in caches to germination is assumed to be 0 at low seed : scatterhoarder ratios, where all caches would be retrieved, and increases with increasing seed : scatterhoarder ratios, where the larger number of caches made increases the chance that some caches would escape recovery. At higher seed : scatterhoarder ratios, animals could stop caching entirely in the face of a surfeit of food, but even if cache rates remained constant, the proportion of the crop surviving in caches would decrease relative to the total seed crop. This model assumes that all seeds would be handled by scatterhoarders at low seed : scatterhoarder ratios and that at ratios between the origin and line X, all seeds handled would eventually be eaten. At seed : scatterhoarder ratios between Lines X and Y, all seeds are handled by scatterhoarders, but the probability that cached seeds survive increases with increasing seed : scatterhoarder ratios. At higher ratios beyond Line Y, some seeds escape detection by scatterhoarders and the number escaping detection increases with increasing seed : scatterhoarder ratio.

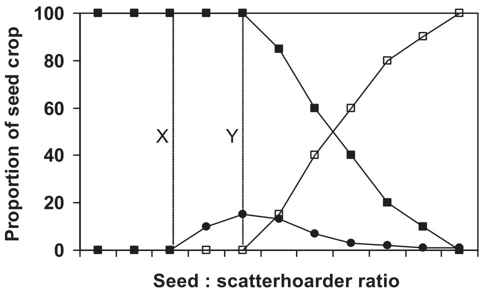

Fig. 17.1. Hypothetical relationship between the proportion of the seed crop handled by scatterhoarders (solid boxes), the proportion escaping handling (open boxes) and the proportion of cached seeds surviving to germination (solid circles) versus the relative abundance of seeds and scatterhoarders (seed : scatterhoarder ratio).

This model is consistent with the hypothesis that the role of scatterhoarders is conditional, depending upon the relative abundance of scatterhoarders and seeds. At low seed : scatterhoarder ratios (below Line X) scatterhoarders act as antagonistic predators. Beyond Line X, scatterhoarders have the potential to act as mutualistic seed dispersers, but this depends upon the relative success of recruitment from seeds that escape scatterhoarders compared to that from seeds cached by scatterhoarders. If a plant species was entirely dependent on scatterhoarders for recruitment (scatterhoarders act as obligate mutualists) the number of seedling recruits would be determined entirely by the number of caches surviving (line with solid circles in Fig. 17.1). This could be the case for seeds that require burial for germination or for seedling establishment but which rarely become buried by other means (Hallwachs, 1986; Smythe, 1989; Forget, 1994; Asquith *et al.*, 1999). Seeds escaping scatterhoarder handling at high crop sizes would contribute nothing to recruitment. However, even this case is conditional, as the obligate mutualist acts as a seed predator at low seed : scatterhoarder ratios.

In contrast, in cases where cached seeds never successfully germinated (scatterhoarders act as seed predators), seedling recruitment would be determined by the probability of seed escape (line with open boxes in Fig. 17.2). This could be the case when small seeds are cached too deeply to

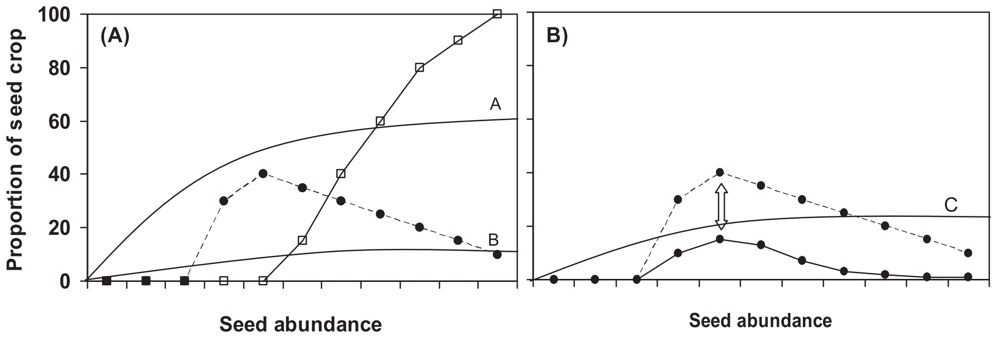

Fig. 17.2. (A) Hypothetical relationship between the proportion of the seed crop that successfully recruits from scatterhoarder caches (solid squares) and the proportion that escapes scatterhoarder handling (open boxes) versus crop size. The potential recruitment of the same plant in the absence of the scatterhoarder could be higher than for scatterhoarder cached seeds (line A) or lower than that of scatterhoarder cached seeds (Line B). (B). If Line C is the probability of seedling recruitment in the absence of scatterhoarders, factors that shift the probability of cache survival from the dashed line (solid circles) to the solid line (solid circles) will cause a shift in the role of scatterhoarders from antagonists to mutualists.

allow them to germinate (Hulme, 2002) or when scatterhoarders excise embryos from cached seeds to prevent them from germinating (Fox, 1982; Steele *et al.*, 2001). This interaction could be conditional if cached seeds could germinate under a special set of conditions, such as a shift in the behaviour of the scatterhoarder to excise embryos under some circumstances but not others.

Although most studies compare the relative success of seeds dispersed by scatterhoarders to undispersed seeds, the overall benefit of scatterhoarding for a plant should be judged by comparing potential seedling recruitment in the absence of scatterhoarders altogether. For example, in Fig. 17.2, I show two scenarios for recruitment in the absence of scatterhoarders as it relates to crop size. In the absence of the scatterhoarder (Line A), recruitment would be greater than that from scatterhoarder caches and scatterhoarders would be poor mutualists. Note that for this model I have assumed for simplicity that the scatterhoarder population remains constant across varying crop sizes and thus use crop size rather than seed:scatterhoarder ratio as the independent variable. I have also assumed that seedling recruitment in the absence of scatterhoarders will increase with increasing crop size but will reach an asymptote as density-dependent factors slow recruitment at high crop sizes.

In situations where seedling recruitment in the absence of scatterhoarders would follow Line A, if scatterhoarders remove the entire seed/fruit crop so that some cached seeds survive but no undispersed seeds escape detection (the shaded area of Fig. 17.2A), an ‘apparent mutualism’ can arise because the only seeds that survive to give rise to seedlings are from rodent caches. In this situation, all seedlings arise from rodent cached seeds and plant dependence on scatterhoarder dispersal seems apparent. However, if recruitment would be higher in the total absence of scatterhoarders, then scatterhoarders have an overall negative effect on potential plant fitness and they act as antagonists. For example, scatterhoarding white-tailed rats on my Australian study plot removed the entire crop of yellow walnut (*Beilschmedia bancroftii*) seeds well before any seeds reached the time for germination (Theimer, 2001). Although none of the subset of rat-cached seeds I followed survived to germination, all seedlings subsequently arose on the study plot from buried seeds that were placed in microsites consistent with being cached there by rats. Thus, all seedlings I found were apparently from rat-cached seeds (Theimer, 2001). In contrast, a subset of 40 seeds fell naturally into a vertebrate exclosure and were subsequently exposed to all natural processes except those caused by terrestrial birds and mammals. Five years later, only two seedlings survived outside the exclosure out of the roughly 300 seeds that were removed by rats (0.7%) (a very conservative estimate based on one line transect at the height of fruit fall). In contrast, of the 40 seeds protected in the exclosure, five seedlings have arisen and are still alive (12%). This suggests that seedling recruitment would be higher in the complete absence of scatterhoarding rats. As a result, rats are effective dispersers in that seedlings apparently arise from rare caches that are not recovered, but they have a negative effect on the potential plant recruitment that would be realized in their absence.

In contrast, if potential recruitment in the absence of scatterhoarders is low relative to that from cached seeds (Line B in Fig. 17.2), then scatterhoarders would act as mutualists and seedling recruitment would be primarily from cached seeds at low crop sizes and from a combination of caches and seeds escaping scatterhoarders at high crop sizes. The mutualism would be conditional, however, under two scenarios. First, if the probability of cached-seed survival changed so that it fell below the number that could potentially be recruited at a given crop size, then scatterhoarders could act as predators under some conditions and mutualists under others. For example, in arid areas, the ability of rodents to detect caches via olfaction depends on soil moisture, with lower detection rates under very dry conditions (Vander Wall, 1993, 1995, 2000). As a result, cache survival could be significantly lower in a moist year compared to a dry year even though scatterhoarder : seed ratios were similar (Fig. 17.2 B) and scatterhoarders could act as antagonists in wet years and as mutualists in dry years. The other scenario under which the mutualism would be conditional is if conditions could cause a shift in the recruitment probability for undispersed seeds, that is, a shift from line B to A in Fig. 17.2, as discussed in the next section.

Conditionality and Variation in Plant Dependence on Scatterhoarders for Recruitment

For plants with seeds that can germinate whether or not they are dispersed by scatterhoarders, the benefit of dispersal must outweigh the often very high cost of seeds eaten by scatterhoarders. In many cases, this is possible because the probability of recruitment in the absence of the scatterhoarder is very small (Line B in Fig. 17.2), often due to abiotic or biotic conditions that limit recruitment. This can occur when: (i) undispersed seeds and the seedlings arising from them suffer high mortality from seed predators or pathogens, and (ii) when scatterhoarders act as directed dispersal agents by moving seeds to specific microsites required for successful plant germination and establishment that seeds would rarely reach by other means (Howe and Smallwood, 1982).

In the first case, the mutualism may be conditional on the presence of the mortality agent acting on undispersed seeds, and the outcome of the interaction can change as the strength of the mortality factor changes. Undispersed seeds of several large-seeded neotropical tree species suffer heavy predation by insects and large vertebrates, and scatterhoarding by rodents may allow escape from these mortality agents (e.g. Janzen, 1971b; Kiltie, 1981; Wright, 1983; Hallwachs, 1986; Smythe, 1989; Forget *et al.*, 1994, Forget, 1996, Wenny, 1999). As a result, if the populations of vertebrate or invertebrate seed predators are altered, the role of scatterhoarding rodents could also change. White-lipped and collared peccaries (*Tayassu pecari* and *Pecari tajacu*) have been implicated as important seed and seedling predators in the neotropics (see Beck, Chapter 6, this volume), but both are subjected to heavy hunting pressure that could potentially change peccary–rodent seed dynamics (Peres, 1996). Silman *et al.* (2003) documented that after peccaries had been extirpated from an area, overall seedling recruitment of *Astrocaryum murumuru* was significantly higher and less reliant on safe-sites near objects. Although they interpreted their results as strong evidence for the impact of peccary seed predators on seedling recruitment, their data also suggest that the importance of rodents scatterhoarding seeds near objects can become less important in the absence of the strongly interacting mortality agent. Given that habitat fragmentation and hunting can greatly reduce peccary populations, loss of this mortality agent from the system could shift the relative importance of rodent scatterhoarders for plant recruitment.

Changes in invertebrate seed predation could also shift in time and space. For example, Janzen (1971b) argued that bruchid attack on *Scheelea* palm seeds would be minimal under young trees that had never fruited and in areas where water could carry seeds some distance from the parent tree. As a result, bruchid effects would vary depending upon palm age and location. Likewise, in areas where peccaries have been reduced by hunting, undispersed seeds of *Carapa procera* (Meliaceae), a subcanopy rainforest tree, suffered heavy mortality via both mammal seed predators and infestation by moths, resulting in the majority of seedling recruitment in most years arising from rodent-dispersed seeds (Forget, 1996). However, in the El Niño year of 1997, moth infestation was relatively low and seedlings established from undispersed seeds (P.-M. Forget, personal communication).

For the case of directed dispersal by scatterhoarders, the strength of the mutualism hinges on the dependence of the plant on specific microsites for establishment. Although microsite dependence is often treated as if it is a fixed requirement, a number of environmental factors can shift the relative importance of microsites for plant establishment and thereby shift the role of scatterhoarders from mutualists to antagonists. I will focus on two examples to illustrate this point, one that illustrates how natural variation can potentially shift the importance of microsites and one that illustrates how anthropogenic effects can do so.

In many semi-arid and arid regions, tree establishment may be facilitated by the presence of nurse shrubs, and movement of seeds by scatterhoarders to sites near nurse structures could be interpreted as directed dispersal to these beneficial microsites (Vander Wall, 1997). In some systems, like that of pinyon pines (*Pinus monophylla* and *Pinus edulis*), burial of seeds as well as movement to nurse shrubs is necessary for seedling establishment (Chambers *et al.*, 1999; Chambers, 2001). Scatterhoarding rodents cache a substantial proportion of seeds in these microsites and therefore act as important mutualists in this system (Vander Wall, 1997). However, movement to nurse shrubs may not be beneficial for all species or under all conditions. Calloway *et al.* (1996) showed that congeneric pines growing in the same area responded very differently to the same nurse plant, with one species benefiting from the association while seedlings of two other species suffered because they were inferior competitors for resources compared to the nurse plant. Within a plant species, the importance of nurse plants could also vary with changing conditions. Recent work in northern Patagonia has shown that establishment of the conifer (*Austrocedrus chilensis*) shows strong climatic variation in nurse dependence, with plant establishment dependent on nurse structures in years with moderate weather and independent of nurse structures in cool, wet years (Kitzberger *et al.*, 2000). Studies of biennial plants (de Jong and Kinkhamer, 1988) and bunchgrasses (Greenlee and Calloway, 1996) likewise showed a shift from facilitation to competition in nurse plant interactions as abiotic conditions changed. Thus, whether movement of seeds to microsites like these by scatterhoarders is a positive or negative interaction for a plant species could be conditional on natural variation in abiotic conditions across space and time.

Anthropogenic changes in natural disturbance regimes could also change plant dependence on microsites and the role of rodent scatterhoarders. In the ponderosa pine forests of the southwestern USA, low intensity ground fires were historically relatively common and would have created unique challenges for seedling survival, but livestock grazing and fire suppression over the past century has changed the conditions recruiting seedlings face (Cooper, 1960; Covington and Moore, 1994). Currently, these forests have higher stem densities and lack the widely spaced clumps of trees that apparently characterized historical forests, suggesting that seedling recruitment has increased in the absence of fire. One way this may have occurred is by changing microsite dependence of ponderosa pine seedlings. White (1985) has argued that in the presence of ground fires, recruitment of ponderosa pine may have required germination in sites that would remain relatively free of fire in successive years. He suggested that when fire consumed downed logs, it created a heavily burned patch that would act as a relatively fire-free island in successive years. We have recently documented that rodent scatterhoarders cache seeds preferentially near downed logs in unburned forests (a pattern similar to that described by Sullivan (1978) for Douglas fir seeds) and differentially move seeds to areas of charred soil in areas that have been burned (Compton and Theimer, in preparation). Seeds buried near logs by scatterhoarders could potentially survive when fire destroys the overlying downed log and later germinate in the kind of safe site White (1985) envisaged. Preliminary experiments we have undertaken by placing seeds in simulated caches near logs and slash piles suggest some seeds could survive these conditions. Alternatively, seeds could be moved to these charred areas subsequent to fire. Scatterhoarders at one of our study sites showed a significant movement of ponderosa pine seeds from uncharred to charred areas (Compton and Theimer, in preparation). In either case, anthropogenic changes in natural fire regimes could have shifted the role of rodents from a historical role of directed dispersal agents that moved seeds to fire-resistant microsites, to the role of primarily seed predators in the absence of fire when seedlings no longer depend on scatterhoarders for dispersal to safe sites. Although this scenario is currently hypothetical, it illustrates the potential for anthropogenic alteration of natural disturbance regimes to change the role of scatterhoarders due to the conditional nature of the interaction.

Potential Effects of Forest Fragmentation on the Conditional Mutualism

Forest fragmentation could potentially alter both the seed : scatterhoarder ratio and the relative ability of seedlings to recruit in the absence of scatterhoarders through its effect on other strongly interacting agents of seed/seedling mortality. The effect on seed : scatterhoarder ratios will depend on both the response of seeding/fruiting trees to fragmentation and the response of the scatterhoarder. In the simplest scenario, if seed producing trees of a particular species were uniformly distributed in undisturbed forest, then the number of trees of that species initially remaining in a forest fragment should be linearly related to fragment size (Line B in Fig. 17.3A). For trees with non-uniform adult distribution, effects of fragmentation would be more idiosyncratic. In species with highly aggregated distributions, for example, relative tree abundance (and therefore seed abundance) could vary unpredictably among fragments of similar size simply because of variation in whether one or more aggregations were included in the fragment. Tree density in fragments could also change through time. Large trees have been shown to experience higher mortality in small fragments (Laurance *et al.*, 2000) and the shift in community composition towards a greater proportion of redural species is also more rapid due to larger edge effects (Tabarelli *et al.*, 1999; Laurance *et al.*, 1998). Finally, the relationship between tree abundance and seed production could be fundamentally altered in fragments if productivity of trees was changed in fragmented habitats (e.g. Ganzhorn, 1995).

Animals also vary in their response to fragmentation (Laurance, 1994; Harrington *et al.*, 2001; see Dennis *et al.*, Chapter 7, this volume), and Fig. 17.3A illustrates four hypothetical responses. Some species are highly sensitive to fragmentation and their

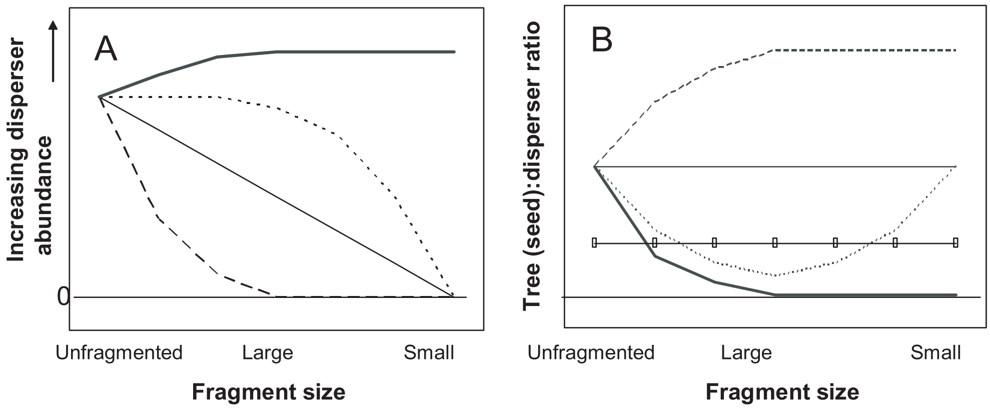

Fig. 17.3. (A) Four of several ways in which scatterhoarder abundance could be altered by fragmentation. Note that degree of fragmentation increases to the right, so fragment size decreases. Light solid line represents a species with abundance that decreases linearly with decreasing fragment size, heavy solid line represents a species that increases with decreasing fragment size, dashed line represents a species with populations that remain stable until a threshold fragment size is reached and the dotted line represents a species with populations that decline rapidly even in relatively large fragments. (B) The hypothetical seed : scatterhoarder ratio for the scatterhoarders described in A if the tree population (and therefore the seed abundance) declines linearly with decreasing fragment size. The box-line represents the hypothetical minimum seed : disperser ratio necessary for seedling recruitment in the presence of scatterhoarders. For scatterhoarder species that either increase with fragmentation (heavy solid line) or remain stable until a threshold is reached (dashed line), seed : scatterhoarder ratios can fall below the level that allows seedling recruitment, and scatterhoarders act as antagonists.

populations decline to low levels in all but the largest fragments (dashed line in Fig. 17.3A), some show populations that decline relatively linearly with decreasing fragment size (solid line in Fig. 17.3A), and some remain stable in large and intermediate fragments and decline only in small fragments (dotted line in Fig. 17.3A). Finally, some species could increase as fragment size decreases, perhaps due to an ability to exploit edge habitats or the surrounding matrix (heavy, solid line in Fig. 17.3A).

For any one scatterhoarding rodent, the effect of fragmentation on its abundance relative to that of seeds could shift its role from seed disperser to seed predator. Figure 17.3B illustrates how the relative abundance of seeds and scatterhoarders could change with fragmentation for a scatterhoarding species exhibiting each of the four responses to fragmentation illustrated in Fig. 17.3A. In this example, for simplicity I have assumed that tree and, therefore, seed abundance decline linearly with decreasing fragment size, but as pointed out above, this function could vary greatly, depending upon spatial distribution of seed-producing trees and the tree response to fragmentation. I have further assumed that there is a ratio of seed : scatterhoarder above which some seeds will survive in caches to germination but below which probability of cache survival approaches zero (e.g. beyond Line X on Fig. 17.1). This model suggests that if the seed : scatterhoarder ratio in continuous forest was above the threshold for seed survival, so that scatterhoarders were effective seed dispersers in these areas, decreasing fragment size would lead to a shift from disperser to predator in two cases. In the first, scatterhoarder species with populations that either remained stable or increased with increasing fragmentation could become so numerous that probability of seed survival falls to 0 and scatterhoarders would act as seed predators. In the second, less intuitive case, scatterhoarder populations that remained stable in large and intermediate fragments and decreased in small fragments could act as predators in the intermediate fragments but return to levels for effective dispersal in smaller fragments.

Several studies suggest that fragmentation could potentially alter the relative abundance of rodents and shift the scatterhoarder : seed ratio (Rosenblatt *et al.*, 1999, Nupp and Swihart, 2000; Donoso *et al.* 2004). For example, biomass of granivorous rodents in the midwestern USA showed a curvilinear relationship with log fragment area, with lowest biomasses occurring in fragments of intermediate size (Nupp and Swihart, 2000). Although scatterhoarding behaviour was not studied, several species known to cache seeds showed the same curvilinear relationship (white-footed mice, *Peromyscus leucopus*, and eastern chipmunks, *Tamias striatus*), while others showed a negative response to decreasing fragment size (grey squirrels, *Sciurus carolinensis*) or no response (fox squirrels, *Sciurus niger*). The model presented here suggests that white-footed mice and chipmunks would act more as seed predators in small fragments and as seed dispersers in intermediate fragments, while fox squirrels would act increasingly as seed predators as fragment sizes decreased. In a similar example where seed fate was monitored, abundance of wood mice (*Apodemus sylvaticus*) in small fragments of Spanish juniper was nearly nine times that in contiguous forest (Santos and Telleria, 1994) and the significantly lower abundance of seedlings in fragments were hypothesized to be the result of increased seed predation by these mice. Studies demonstrating idiosyncratic effects of fragmentation on the seed–scatterhoarder interaction could be due in part to natural variation in seed : scatterhoarder ratios among and within fragments and intact forest, or to variation in the effects on other strongly interacting agents.

Because the seed–scatterhoarder mutualism is often dependent on strong interaction from other biotic agents like seed predators and pathogens, the response of these interactors to fragmentation can alter the relative dependence on scatterhoarding for tree recruitment. If the seed predators or pathogens that lower recruitment in intact forest are absent in fragments, potential tree recruitment in the absence of scatterhoarders could increase (e.g. shift from Line B to A in Fig. 17.2) and scatterhoarders would no longer act as mutualists. For example, Pizo (1997) showed that rodent densities and insect seed predators varied markedly between a large (49,000 ha) reserve and a small (250 ha) fragment.

The outcome of seed–scatterhoarder interactions in both fragmented and continuous forest will be complicated by community interactions (e.g. Dennis *et al.*, Chapter 7, this volume). From the plant perspective, the relative value of seeds of any one tree species compared to others in the fragment or the surrounding matrix could result in frequency dependent foraging behaviour by the scatterhoarder (Hulme, 1996; Hulme and Hunt, 1999; Hoshizaki and Hulme, 2002). For example, if the seeds of two plant species were equally abundant in an area, and both were known to be cached by a scatterhoarder, the seed : scatterhoarder ratio could be approximated by combining the abundances of both plant species. However, if the seeds of one species was strongly preferred over the other, the effective seed : scatterhoarder ratio experienced by the preferred species could be considerably lower than for the less preferred species, altering the probability of recruitment and the outcome of the seed–scatterhoarder interaction. Likewise, the total abundance of all species competing for seeds may be a better estimator of the probability of cache survival in some cases, as scatterhoarders may experience much smaller realized crop sizes in the presence of competing species than in their absence. Finally, overall cache survival could be lowered in areas with species that can pilfer caches but do not create them.

Short-term versus Long-term Conditionality in Mutualism: When Does the Paradigm Matter?

Considering the seed scatterhoarder system as a conditional mutualism because rodents act as seed predators at low seed : scatterhoarder ratios and as dispersers at high ratios could be considered as trivial as considering trees mutualists of rodents when they produce seeds and as antagonists when they do not. However, it is exactly within such temporally and spatially limited contexts that many studies are forced to attempt to define the relationship. As a result, recognizing the short-term conditionality of the relationship could help explain the significant variation in the outcomes of the interaction over small spatial scales and the inconsistent response when comparing fragmented and continuous landscapes (Hallwachs, 1986; Asquith *et al.*, 1999; Wright *et al.*, 2000; Chauvet, 2001; Feer and Forget, 2002).

The evolutionary role that scatterhoarders play will be determined by the outcome of the interaction averaged over broad spatial scales and long time periods. As a result, the conditional mutualism paradigm would be most important when it suggests how anthropogenic effects may alter long-established interactions (Fig. 17.4). Three examples described in this chapter are relevant in this context:

1. The potential for human-induced climate change to alter the importance of directed dispersal to nurse plants;
2. The potential for disruption of natural fire cycles in fire-adapted communities to change the conditions for successful recruitment and thereby the importance of scatterhoarders as mutualists;
3. The disruption of long-standing seed–seed, predator–scatterhoarder interactions through hunting and habitat fragmentation.

Ultimately, the value of a conceptual model like that of conditional mutualism depends on its ability to define new avenues of research and alter our view of system interactions. The utility of this approach applied to scatterhoarding rodents is that it focuses attention on those general conditions that may affect their role and highlights how both natural variation and anthropogenic changes could interact to change those conditions. Finally, it underscores the importance of verifying system and site specific interactions (e.g. Hoshizaki *et al.*, 1999) and cautions against generalizations about the role of a scatterhoarder species based on studies carried out under different abiotic or biotic conditions.

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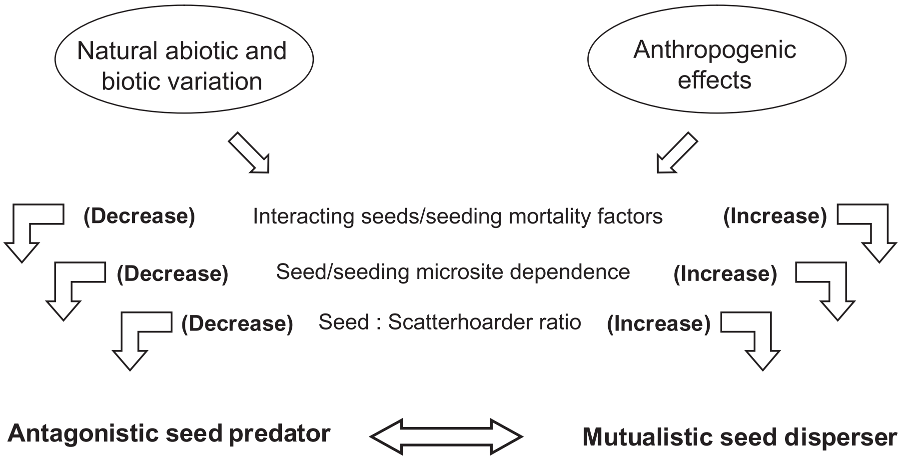

Fig. 17.4. The conditional nature of the role of scatterhoarding rodents along the continuum from antagonistic seed predators to mutualistic seed dispersers depends whether anthropogenic and natural variation increases or decreases seed and scatterhoarder abundances, interacting mortality agents of seeds and seedlings and microsite dependence.

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References

Asquith, N.M., Terborgh, J., Arnold, A.E. and Riveros, C.M. (1999) The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. *Journal of Tropical Ecology* 15, 229–235.

Billick, I. and Tonkel, K. (2003) The relative importance of spatial vs. temporal variability in generating a conditional mutualism. *Ecology* 84, 289–295.

Bronstein, J.L. (1994) Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution* 9, 214–217.

Calloway, R.M., Delucia, E.H., Moore, D., Nowak, R. and Schlesinger, W.H. (1996) Competition and facilitation: contrasting effects of *Artemesia tridentata* on desert vs. montane pines. *Ecology* 77, 2130–2141.

Chambers, J.C. (2001) *Pinus monophylla* establishment in an expanding *Pinus–Juniperus* woodland : environmental conditions, facilitation and interacting factors. *Journal of Vegetation Science* 12, 27–40.

Chambers, J.C., Vander Wall, S.B. and Schupp, E.W. (1999) Seed and seedling ecology of pinon and juniper species in the pygmy woodlands of western North America. *The Botanical Review* 65, 1–36.

Chauvet, S. (2001) Effects of forest fragmentation on plant-animal interactions: consequences for plant regeneration. PhD thesis, University of Paris VI, Paris, France.

Cooper, C.F. (1960) Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecological Monographs* 30, 129–164.

Covington, W.W. and Moore, M.M. (1994) Southwestern ponderosa pine forest structure: changes since Euro-American settlement. *Journal of Forestry* 92, 39–47.

Cushman, J.H. and Whitham, T.G. (1989) Conditional mutualism in a membracid-ant association: temporal, age-specific, and density-dependent effects. *Ecology* 70, 1040–1047.

De Jong, T.J. and Klinkhamer, P.G. (1988) Seedling establishment of biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand-dune area: the importance of water for differential survival and growth. *Journal of Ecology* 76, 393–402.

De Steven, D. and Putz, F.E. (1984) Impact of mammals on early recruitment of a tropical tree. *Oikos* 43, 207–216.

Donoso, D.S., Grez, A.A. and Simonetti, J.A. (2004) Effects of forest fragmentation on the granivory of differently sized seeds *Biological Conservation* 115, 63–70.

Feer, F. and Forget, P.-M. (2002) Spatio-temporal variations in post-dispersal seed fate. *Biotropica* 34, 555–566.

Forget, P.-M. (1996) Removal of seeds of *Carapa procera* (Meliceae) by rodents and their fate in rainforest in French Guiana. *Journal of Tropical Ecology* 12, 751–761.

Forget, P.-M. (1990) Seed dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. *Journal of Tropical Ecology* 6, 459–468.

Forget, P.-M. (1994) Recruitment pattern of *Voucapa americana* (Caesalpinaceae), a rodent-dispersed tree species in French Guiana. *Biotropica* 26, 408–419.

Forget, P.-M., Munoz, E. and Leigh, E.G. Jr (1994) Predation by rodents and bruchid beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panama. *Biotropica* 26, 420–426.

Forget, P.-M., Hammond, D., Milleron, T. and Thomas, R. (2001) Seasonality of fruiting and food hoarding by rodents in Neotropical forests: consequences for seed dispersal and seedling recruitment. In: Levey, D.J., Silva W.R. and Galetti, M. (eds) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, UK, pp. 241–246.

Fox, J.F. (1982) Adaptation of gray squirrel behavior to autumn germination by white oak acorns. *Evolution* 36, 800–809.

Ganzhorn, J.U. (1995) Low-level forest disturbance effects on primary production, leaf chemistry and fruiting. *Ecology* 76, 2084–2096.

Greenlee, J. and Calloway, R.M. (1996) Effects of abiotic stress on the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *American Naturalist* 148, 386–396.

Hadj-Chikh, L.Z., Steele, M.A. and Smallwood, P.D. (1996) Caching decisions by grey squirrels: a test of the handling-time and perishability hypotheses. *Animal Behaviour* 52, 941–948.

Hallwachs, W. (1986) Agoutis (*Dasyprocta punctata*) the inheritors of guapinol (*Hymenaea* *courbaril*: Leguminosae). In: Estrada, A. and Fleming, T.H. (eds). *Frugivores and Seed Dispersal*. Dr. W. Junk Publishers, Dordrecht, The Netherlands, pp. 285–304.

Harrington, G.N., Freeman, A.N.D. and Crome, F.H.J. (2001) The effects of fragmentation of an Australian tropical rain forest on populations and assemblages of small mammals. *Journal of Tropical Ecology* 17, 225–240.

Herrera, C.M. and Jordano, P. (1981) *Prunus mahaleb* and birds: the high efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs* 51, 203–218.

Hoshizaki, K., Suzuki, W. and Nakashizuka, T. (1999) Evaluation of secondary dispersal in a large-seeded tree *Aesculus turbinata*: a test of directed dispersal. *Plant Ecology* 144, 167–176.

Hoshizaki, K. and Hulme, P.E. (2002) Mast seeding and predator-mediated indirect interactions in a forest community: evidence from post-dispersal fate of rodent-generated caches. In: Levey, D.J., Silva, W.R. and Galetti, M. (eds) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, UK, pp. 227–239.

Howe, H.F. and Smallwood, P.D. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13, 201–238.

Hulme, P.E. (1996) Natural regeneration of yew (*Taxus baccata* L.): microsite, seed or herbivore limitation? *Journal of Ecology* 84, 853–861.

Hulme, P.E. (2002) Seed-eaters: seed dispersal, destruction and demography. In: Levey, D.J., Silva, W.R. and Galetti, M. (eds) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, UK, pp. 257–271.

Hulme, P.E. and Hunt, M.K. (1999) Rodent post-dispersal seed predation in deciduous woodland: predator response to absolute and relative abundance of prey. *Journal of Animal Ecology* 68, 417–428.

Janzen, D.H. (1971a) Seed predation by animals. *Annual Review of Ecology and Systematics* 2, 465–492.

Janzen, D.H. (1971b) The fate of *Scheelea rostrata* fruits beneath the parent tree: predispersal attack by bruchids. *Principes* 15, 89–101.

Janzen, D.H. (1981) *Enterolobium cyclocarpum* seed passage rate and survival in horses, Costa Rican Pleistocene seed dispersal agents. *Ecology* 62, 593–601.

Kiltie, R.A. (1981) Distribution of palm fruits on a rain forest floor: why white-lipped peccaries forage near objects. *Biotropica* 13, 141–145.

Kitzberger, T., Steinaker, D.F. and Veblen, T.T. (2000) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology* 81, 1914–1924.

Laurance, W.F. (1994) Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. *Biological Conservation* 69, 23–32.

Laurance, W.F., Ferreira, L.V., Rankin-DeMerona, J.M., Laurance, S.G., Hutchings, R.W. and Lovejoy, T.E. (1998) Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12, 460–464.

Laurance, W.F., Delamonica, P., Laurance, S.G., Vascocelos, H.L. and Lovejoy, T.E. (2000) Rainforest fragmentation kills big trees. *Nature* 404, 836.

Nupp, T.E. and Swihart, R.K. (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy* 81, 512–526.

Peres, C.A. (1996) Population status of white-lipped and collared peccaries in hunted and unhunted Amazonian forests. *Biological Conservation* 77, 115–123.

Peres, C.A., Schiesari, L.C. and Dias-Leme, C.L. (1997) Vertebrate predation of Brazil-nuts (*Bertholletia excelsa*, Lecythidaceae), an agouti-dispersed Amazonian seed crop: a test of the escape hypothesis. *Journal of Tropical Ecology* 13, 69–79.

Pizo, M.A. (1997) Seed dispersal and predation in two populations of *Cabralea canjerana* (Meliaceae) in the Atlantic forest of south-eastern Brazil. *Journal of Tropical Ecology* 13, 559–578.

Rosenblatt, D.L., Heske, E.J., Nelson, S.L., Barber, D.M., Miller, M.A. and MacAllister, B. (1999) Forest fragments in east-central Illinois: islands or habitat patches for mammals? *American Midland Naturalist* 141, 115–123.

Santos, T. and Telleria, J.L. (1994) Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper *Juniperus thurifera*. *Biological Conservation* 70, 129–134.

Schupp, E.W. (1990) Annual variation in seedfall, postdispersal predation, and recruitment of a neotropical tree. *Ecology* 71, 504–514.

Schupp, E.W. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108, 15–29.

Silman, M.R., Terborgh, J.W. and Kiltie, R.A. (2003) Population regulation of a dominant rain forest tree by a major seed predator. *Ecology* 84, 431–438.

Silvertown, J.W. (1980) The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* 14, 235–250.

Smythe, N. (1970) Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *American Naturalist* 104, 25–35.

Smythe, N. (1989) Seed survival in the palm *Astrocaryum standleyanum*: evidence for dependence upon its seed dispersers. *Biotropica* 21, 50–56.

Sork, V.L. (1993) Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp). *Vegetatio* 107/108, 133–147.

Steele, M.A., Turner, G., Smallwood, P.D., Wolff, J.O. and Radillo, J. (2001) Cache management by small mammals: experimental evidence for the significance of acorn-embryo excision. *Journal of Mammalogy* 82, 35–42.

Sullivan, T.P. (1978) Lack of caching of direct-seeded Douglas-fir seeds by mice. *Canadian Journal of Zoology* 56, 1214–1216.

Tabarelli, M., Montovani, W. and Peres, C. (1999) Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* 10, 119–127.

Theimer, T.C. (2001) Seed scatterhoarding by white-tailed rats: consequences for seedling recruitment by an Australian rain forest tree. *Journal of Tropical Ecology* 17, 177–189.

Vander Wall, S.B. (1990) *Food Hoarding in Animals*. The University of Chicago Press, Chicago, Illinois, 445 pp.

Vander Wall, S.B. (1993) Cache site selection by chipmunks (*Tamias* spp) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*). *Oecologia* 96, 246–252.

Vander Wall, S.B. (1995) Influence of substrate water on the ability of rodents to find buried seeds. *Journal of Mammalogy* 76, 851–856.

Vander Wall, S.B. (1997) Dispersal of singleleaf pinon pine (*Pinus monophylla*) by seed-caching rodents. *Journal of Mammalogy* 78, 181–191.

Vander Wall, S.B. (2000) The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology* 11, 544–549.

Vander Wall, S.B. (2002) Masting in animal-dispersed pines facilitates seed dispersal. *Ecology* 83, 3508–3516.

Wenny, D.G. (1999) Two stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica. *Journal of Tropical Ecology* 5, 481–496.

White, A.S. (1985) Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* 66, 589–594.

Wright, S.J. (1983) The dispersion of eggs by a bruchid beetle among *Scheelea* palm seeds and the effect of distance to the parent palm. *Ecology* 65, 1016–1021.

Wright, S.J., Zeballos, H., Dominguez, I., Gallardo, M.M., Moreno, M.C. and Ibanez, R. (2000) Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology* 14, 227–239.