

Review

How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals

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Some plants that are dispersed by scatter-hoarding animals appear to have evolved the ability to manipulate the behaviour of those animals to increase the likelihood that seeds and nuts will be stored and that a portion of those items will not be recovered. Plants have achieved this in at least four ways. First, by producing large, nutritious seeds and nuts that are attractive to animals and that stimulate hoarding behaviour. Second, by imposing handling costs that cause animals to hoard rather than to eat items immediately. These handling costs can take one of two forms: physical barriers (e.g. hard seed coats) that take time to remove and secondary chemicals (e.g. tannins) that impose metabolic costs. Third, by masting, where a population of plants synchronizes reproductive effort, producing large nut crops at intervals of several years. Mast crops not only satiate seed predators, but also increase the amount of seed dispersal because scatter-hoarding animals are not easily satiated during caching (causing animals to store more food than they can consume) but are satiated during cache recovery. And fourth, by producing seeds that do not emit strong odours so that buried seeds are less likely to be discovered. These, and perhaps other, traits have increased the relative success of plant species with seeds dispersed by scatter-hoarding animals.

Keywords: coevolution; food handling; masting; scatter hoarding; seed dispersal; species interactions

1. INTRODUCTION

Over the past half century, scatter-hoarding animals have become important objects for the study of behaviour (e.g. Roberts 1979; Smith & Reichman 1984; Kallander & Smith 1990; Vander Wall 1990; Smulders 1998; Vander Wall & Jenkins 2003; Dally *et al.* 2006). Studies have ranged from descriptions of how animals prepare individual caches (Haftorn 1956; Kallander 1978; Bossema 1979; Kawamichi 1980; Pravosudov 1986), to how animals secure resources and thereby increase their competitive abilities (Stapanian & Smith 1978, 1984; Clarkson *et al.* 1986; Henry 1986; Daly *et al.* 1992; Waite & Reeve 1995; Moore *et al.* 2007), to how animals use stored resources to promote survival or reproduction (Balgooyen 1976; Kuhn & Vander Wall 2008; Landry-Cuerrier *et al.* 2008), to investigations of spatial memory and cognition (Sherry *et al.* 1981; Vander Wall 1982, 1991; Kamil & Balda 1985; Jacobs & Liman 1991; Clayton & Krebs 1994; Bednekoff *et al.* 1997; Pravosudov 2003). Most attention has been focused on how behaviour contributes to an adaptive syndrome for surviving periods of food scarcity.

When the stored food items are seeds, animals that scatter hoard in the ground can be important agents of seed dispersal. The dispersal of propagules by

seed-caching animals such as corvids and rodents is recognized as an important seed-dispersal syndrome (van der Pijl 1969) in temperate and tropical plant communities (Bossema 1979; Forget 1992, 1993; Vander Wall 2001; Johnson *et al.* 2003). This syndrome is exhibited by numerous species of trees (Darley-Hill & Johnson 1981; Sork 1983; Jansen *et al.* 2004; Xiao *et al.* 2005*b*; Vander Wall 2008), shrubs (Vander Wall 1994*b*; Roth & Vander Wall 2005) and even a few grasses and forbs (Longland *et al.* 2001; Borchert 2004).

Although the benefits of scatter hoarding to plants can be considerable, those benefits have often been viewed as incidental to the activities of animals. In this view, dispersed seeds are those that are buried in favourable situations and forgotten, and the plant has little or no control over those events. This form of seed dispersal works because animals are imperfect foragers. The purpose of this contribution is to argue that plants that are adapted to this mode of seed dispersal can increase the likelihood that their propagules will be dispersed by seed-caching animals. They do this in two ways: (i) by increasing the probability that propagules will be buried and (ii) by increasing the likelihood that a buried propagule will not be removed. Animals, of course, do not have any interest in increasing plant fitness. If plants are to influence their own fitness through the behaviour of scatter-hoarding animals, they must do so by producing propagules with traits that cause animals to behave in a way that benefits the plant.

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2. SIZE AND NUTRITIONAL CONTENT OF PROPAGULES

Most of the propagules stored by animals are relatively large and nutritious, and, in fact, large nuts appear to stimulate caching behaviour. Both intra- and inter-specifically, small seeds and nuts have a greater chance of being eaten while large seeds and nuts have a greater chance of being scatter hoarded (Forget *et al.* 1998; Jansen *et al.* 2002, 2004; Xiao & Zhang 2006; Vander Wall 2008; Zhang *et al.* 2008), although other nut traits (e.g. fat or tannin content) can alter this general pattern (Xiao & Zhang 2006; see below). Larger nuts and seeds are usually carried greater distances to cache sites (Hallwachs 1986; Vander Wall 1995; Jansen *et al.* 2002, 2004; Xiao *et al.* 2004, 2005a; Takahashi *et al.* 2007; Zhang *et al.* 2008); however, a few studies (Brewer 2001; Xiao *et al.* 2004) have failed to observe this behaviour. Large nuts also have longer residence times in caches (Jansen *et al.* 2002), and large nuts often demonstrate increased fitness (Jansen *et al.* 2004). For example, larger *Quercus serrata* acorns have longer cache lifetimes and are more likely to produce seedlings in spring (Xiao *et al.* 2004); however, this was not true for larger acorns of *Quercus liaotungensis* (Zhang *et al.* 2008).

A number of selective forces determine propagule size, most notably requirements for germination and establishment of seedlings (Harper *et al.* 1970; Janzen 1971; Saverimuttu & Westoby 1996; Vander Wall 2001). But preference for large seeds and nuts by scatter-hoarding dispersers has no doubt played a role in the evolution of large propagules (Smith & Reichman 1984; Jansen *et al.* 2002). The reason that animals preferentially cache larger nuts and carry them further is not entirely clear. Spacing cached items to protect them from pilferage is clearly important (e.g. Stapanian & Smith 1978), but change in profitability of a nut with change in nut size is probably also important. The value of a nut is proportional to its mass (e.g. caloric content, nutritional reward) but profitability incorporates handling time and travel time (e.g. energy gained/time invested) (Stephens & Krebs 1986). Although it does not appear to have been examined experimentally, the time invested in transporting and caching a nut makes it more profitable to transport and scatter hoard larger nuts. This is especially true when only one item can be carried at a time, as is the case for most animals that scatter hoard large nuts. The food value of small nuts might not warrant a large investment of time, so small nuts are more often eaten or moved only short distances.

3. THE HANDLING COSTS HYPOTHESIS

A second way in which a plant can influence an animal's likelihood of storing a nut is to impose a handling cost. Handling costs can take two forms. First, a physical barrier (e.g. hard endocarp or shell) can slow the rate at which an animal can consume a nut. A long handling time means that it takes considerably longer for an animal to eat a nut than to store it. A forager must decide whether to incur that cost (e.g. lost opportunities to engage in other activities,

increased risk of predation) immediately or defer the cost to some future time by storing the nut. Second, a chemical in the nutmeat can incur a physiological or metabolic cost to the animal after the seed has been consumed. For example, tannins (a large family of polyphenolic compounds found in acorns; *Quercus* and *Lithocarpus*) at high concentrations have a variety of detrimental effects on herbivores and granivores. Their bitter taste acts as a feeding deterrent. If foods with tannins are eaten, the tannins precipitate proteins in the food as well as the digestive enzymes, thereby inhibiting protein digestion and absorption. Chung-MacCoubrey *et al.* (1997) found a negative correlation between tannin content and protein digestibility in acorns. At high concentrations, tannins can also damage gut epithelium and liver and kidney tissues (Fleck & Layne 1990; Chung-MacCoubrey *et al.* 1997). Finally, tannins at high levels can incur metabolic costs because of increased detoxification requirements (Chung-MacCoubrey *et al.* 1997). It is possible that these combined effects could impair performance in ways unrelated to feeding (e.g. locomotion, cognition) that could increase the risk of predation, but these possible effects have not been studied. Many granivorous animals cannot be sustained on a diet of acorns that contain high levels of tannins (Koenig & Heck 1988; Briggs & Smith 1989; Koenig 1991; Chung-MacCoubrey *et al.* 1997). The presence of secondary chemicals can act to reduce the immediate value of food, decreasing the likelihood that a seed-caching animal will eat it, but as the food still has potential value during some future period of food scarcity, the animal is likely to store it.

In the case of handling time, if it takes longer to eat a nut than it does to store it, then a partially satiated animal that finds a nut would be more likely to cache that nut than to eat it (Jacobs 1992b). There have been relatively few tests of this hypothesis. Jacobs (1992b) demonstrated that it took Eastern gray squirrels (*Sciurus carolinensis*) more time to eat a hazelnut (*Corylus* sp.) than to store it, and that squirrels were more likely to scatter hoard hazelnuts with a shell than hazelnuts with the shell removed. The hard shell of hazelnuts significantly increased the time to consume a nut, and squirrels acted to defer that investment of time by storing the nut if they were not hungry. Jacobs (1992b) argued that the squirrels' responses did not appear to be caused by differences in perishability of the two seed types. Cristol (2001) found that crows (*Corvus brachyrhynchos*) cached more California black walnuts (*Juglans hindsii*) than Persian (English) walnuts (*Juglans regia*). Persian walnuts have higher energy content and are much easier to open than black walnuts. They also cached more intact than cracked walnuts of either species, apparently because the cracked nuts required less handling time. Xiao *et al.* (2006a,b) and Xiao & Zhang (2006) found that *Lithocarpus harlandii* (hard shell and long handling time) are more likely to be cached than the nuts of five other species of nut-bearing trees with soft shells and shorter handling times. Hadj-Chikh *et al.* (1996) compared the choice of Eastern gray squirrels for several species of acorns and found little support for the handling time hypothesis, but their

experiment is more relevant to the effects of secondary chemicals on hoarding behaviour (see below).

Many nuts that are adapted for dispersal by seed-caching animals have thick, hard seed coats that animals must invest considerable time to remove (e.g. Smith & Follmer 1972). Examples include walnuts (*Juglans* sp.), hickories (*Carya* sp.), Brazil nuts (*Bertholletia excelsa*), almonds (*Prunus* sp.) and certain pines (*Pinus* sp.). For jays, even the relatively soft hulls of acorns and chestnuts (*Castanea* sp.) require considerable time and energy to remove (e.g. Bossema 1979). An extreme example is black walnut (*Juglans nigra*), whose convoluted cotyledons are very time consuming to remove from the very hard, tight-fitting shell (Smith & Follmer 1972). The hard shells of nuts no doubt act to protect the seed from insects and granivorous vertebrates that do not act as agents of seed dispersal; however, an additional function, which has not been fully appreciated, is that these physical barriers increase the handling time and could influence the decision of scatter-hoarding animals to cache rather than eat a nut.

Acorns have been useful tools in the study of the effect of secondary chemistry on the decision to cache or eat an acorn because different types of acorns have different levels of tannins. Further, in North America, tannin level is correlated with several other important seed traits: most red oak (RO; section *Erythrobalanus*) acorns are characterized by high tannins, high fat content and winter dormancy (i.e. germinate in the spring), whereas white oak (WO; section *Quercus*) acorns usually have lower tannins, lower fat content and lack winter dormancy (i.e. germinate in the autumn) (Smallwood & Peters 1986). A variety of studies have reported that Eastern gray squirrels and other animals consistently scatter hoard RO acorns in preference to WO acorns, which they are more likely to eat (e.g. Hadj-Chikh *et al.* 1996; Ivan & Swihart 2000; Smallwood *et al.* 2001; Steele *et al.* 2006). To help disentangle the potentially confounding effects of tannin concentration, fat content and germination schedules on Eastern gray squirrel foraging decisions, Smallwood & Peters (1986) constructed artificial 'acorns' from chestnut oak (*Quercus prinus*; WO group) acorn meal with different amounts of tannins and fat added (i.e. different handling costs and nutritional reward) and found that in the autumn squirrels were more likely to eat 'acorns' low in tannins (like WO acorns). Although caching was not a part of this study, squirrels cached only 'acorns' that resembled the RO type. During the winter (i.e. during the period of food scarcity), the effect of tannin level on 'acorn' discrimination was markedly reduced.

The effect of tannins on hoarding behaviour is similar in other ecosystems. Free-ranging Edward's long-tailed rats (*Leopoldamys edwardsi*) and chestnut rats (*Niviventer fulvescens*) were more inclined to eat Henry's chestnuts (*Castanea henryi*) and more likely to scatter hoard cork oak (*Quercus variabilis*) acorns at a site in southwest China (Xiao *et al.* 2008). Despite the fact that these two nut species occur in different genera, they have similar compositions (nutritional content) and size but *Q. variabilis* acorns have approximately 20 times

higher tannin content. High tannin levels act as a cue for scatter hoarding (Smallwood & Peters 1986; Hadj-Chikh *et al.* 1996; Xiao *et al.* 2008; but see Steele *et al.* 2001; Xiao *et al.* 2006a,b).

Nuts belonging to other taxa have a variety of different secondary chemicals that influence the decision to eat versus hoard a nut. For example, Guimaraes *et al.* (2003) found that quinolizidine alkaloids in the seeds of *Ormosia arborea* in southern Brazil reduced the likelihood that those seeds would be eaten by red-rumped agoutis (*Dasyprocta leporina*) without affecting the probability that they would be scatter hoarded. Horse chestnuts (*Aesculus turbinata*) contain saponins, which are bitter, reduce palatability and can be toxic (Shimada 2001), but the effect of these chemicals on the decision to eat versus cache those nuts is unknown.

The effect of increasing handling costs (either handling time or secondary chemistry) is to reduce the profitability of a nut relative to other foods in the environment (Janzen 1971). As handling costs go up, the preference ranking of a nut should go down. This preference rank gradually increases as the season of food scarcity deepens (e.g. later in winter or dry season) as foragers gradually deplete more preferred foods. However, the profitability of those nuts appears to remain unchanged. Tannin concentrations in acorns, for example, do not decline significantly during storage in the ground (Koenig & Faeth 1998; Smallwood *et al.* 2001), so handling costs still need to be paid when the acorn is recovered. The persistence of secondary chemicals in other types of nuts during storage still remains to be determined. But species of nuts and seeds with shorter handling times or lower levels of secondary chemicals are probably more likely to be recovered by scatter-hoarding animals during winter and eaten than those nuts and seeds with longer handling times or high levels of secondary chemicals. Consequently, handling costs are likely to have two distinct and separate effects on caching behaviour: (i) increase the likelihood that a nut will be cached and (ii) decrease the likelihood that that nut will be eventually retrieved from the cache site and eaten.

Most of those that have tested the handling time hypothesis (Jacobs 1992b; Hadj-Chikh *et al.* 1996; Cristol 2001) did not follow the ultimate fates of cached nuts; they were interested in handling time from the perspective of animal behaviour and not plant-animal interactions. But Xiao *et al.* (2008) did follow the fates of chestnuts and acorns scatter hoarded by Edward's long-tailed rats and chestnut rats and found that the high-tannin nuts were not only more likely to be stored but were also more likely to survive to become seedlings.

There are several alternative explanations for tannins in nutmeats. One explanation is that secondary chemicals in nuts and seeds are there to defend those propagules against animals that act strictly as seed predators (e.g. insects) and to suppress the growth of microbes (Janzen 1971). Likewise, the heavy seed coat of nuts serves to prevent numerous animals that are not legitimate seed dispersers from gaining access to the edible nutmeat (e.g. Schroger 1960). Those traits that discourage animals that act strictly as seed

predators also, incidentally, reduce the foraging efficiency of legitimate agents of seed dispersal (Smith & Follmer 1972; Lewis 1982; Cristol 2001). These perspectives and the handling costs hypothesis presented here are not mutually exclusive ideas, but the negative effects of secondary chemicals and hard nut shells on legitimate dispersal agents should not be viewed simply as the maladaptive consequences of traits that have evolved to reduce the effectiveness of seed predators and microbes. Physical and chemical traits that reduce the foraging efficiency of scatter-hoarding animals could also benefit the plant by shifting behaviour of those animals from eating to caching.

Some have suggested that the primary reason that gray squirrels cache dormant (spring germinating), high-tannin RO acorns and eat more perishable (autumn germinating), low-tannin WO acorns is to maximize long-term (seasonal as opposed to immediate) energy gain (Smallwood & Peters 1986; Smallwood *et al.* 2001; Steele *et al.* 2001). By eating perishable acorns and storing less perishable acorns, squirrels make more efficient use of resources during winter. This may be one advantage of preferentially caching RO acorns, but it does not explain why RO acorns have high tannin levels relative to WO acorns. Tannins do not contribute to seed dormancy. In China, where acorns do not fall neatly into the RO and WO types, Xiao *et al.* (2008) found that Edward's long-tailed rats preferentially scatter hoard high-tannin *Q. variabilis* acorns despite the fact that they germinate in the autumn (i.e. contrary to the perishability hypothesis). Further, the rats preferred to eat immediately low-tannin *C. henryi* nuts, which do not germinate early. These rats appear to be maximizing short-term energy gains while avoiding the toxic effects of tannins. Smallwood & Peters (1986) and Hadj-Chikh *et al.* (1996) have argued that gray squirrels use high tannin levels as a cue when deciding whether to store an acorn, but have suggested that the squirrels are not avoiding tannins (which they can detoxify) when caching an RO acorn. But why should squirrels pay the high cost of detoxifying tannins in RO acorns if they do not need to?

Seed-caching animals appear to scatter hoard nuts rather than eat them to avoid the negative effects of secondary compounds and/or long handling times. This behaviour is promoted by the unpredictable nature of future seasons of food scarcity. Animals often store more food than they require to survive a season of food scarcity because they cannot know months in advance the duration of a period of food scarcity, the future availability of alternative foods, or the amount of stored food that will be lost to pilferers and microbes. Storage of excess food is insurance against uncertainty. In bountiful years, some animals store more food than they could possibly consume (Chettleburgh 1952; Vander Wall & Balda 1977; Ligon 1978; Darley-Hill & Johnson 1981; Tomback 1982; Vander Wall 1988; §4). Before a period of food scarcity, seeds and nuts with large handling costs still have value, making it advantageous to store them. If high-cost (low preference) items are needed at some future time, then the hoarder can retrieve them and pay the cost. If they are not required, they go unused. This latter fate is, of course, beneficial to plants.

4. MASTING

Masting is the synchronous production of seeds at long intervals by a population of plants (Janzen 1971). Many nut-bearing trees and shrubs that are dispersed by seed-caching animals mast seed, with large seed crops at intervals of 3–5 years separated by years of small to very small seed crops (e.g. Koenig *et al.* 1994). During mast years, nut crops are synchronized over large geographical areas (Koenig & Knops 2000). A number of hypotheses have been offered to explain this phenomenon (Kelly 1994; Kelly & Sork 2002). Those hypotheses that have received the most attention and empirical support are the 'predator satiation hypothesis' and the 'wind pollination hypothesis'. The predator satiation hypothesis asserts that inter-annual variation in seed production prevents specialist seed predators (e.g. insects, granivorous rodents) from tracking a seed population; populations of seed-eating animals decline sharply when few seeds are available, and later when seeds are produced in abundance, the populations of seed predators cannot reproduce quickly enough to consume all the seeds (Sork 1983, 1993; Nilsson 1985; Kelly & Sork 2002). Consequently, more seeds are likely to survive and germinate following a mast year than in the intervening non-mast years. For the pollination hypothesis, synchronized flower production in wind-pollinated plants is credited with increasing seed set (Smith *et al.* 1990; Kelly *et al.* 2001). Most nut-bearing trees in the temperate zone are wind pollinated (Vander Wall 2001).

A third explanation, the 'seed-dispersal hypothesis', has received little support until recently. Some have argued that masting would be a disadvantageous trait in animal-dispersed plants because alternately swamping and then starving one's seed dispersers would probably result in less seed dispersal (e.g. Ims 1990; Herrera *et al.* 1998; Kelly & Sork 2002). Plants should benefit by providing seed-dispersing mutualists with a constant and predictable food supply. This appears to be true for some plants that are dispersed by frugivores but not for those dispersed by seed-caching animals. Although satiating a frugivore would probably result in disproportionately reduced seed dispersal (Ballardie & Whelan 1986; Herrera *et al.* 1994; Levey & Benkman 1999; but see Gorchoff 1988), animals that store nuts are not easily satiated (Vander Wall 2002). Typically, when an animal that stores food encounters a rich supply of nuts, it eats one or two and then stores the rest.

One key piece of evidence needed to support the seed-dispersal hypothesis is that a higher fraction of the seed or nut crop must be dispersed in mast years than would be observed in non-mast years (Kelly & Sork 2002). Some have compared nut removal rates during mast and non-mast years to estimate the effect of masting on the fraction of the nut crop that scatter-hoarding animals harvest (and presumably store). Typically, removal of experimental nuts and seeds is slower in the mast years (Crawley & Long 1995; Theimer 2001; Li & Zhang 2007). For example, Xiao *et al.* (2005b) found that removal rates of experimental *Castanopsis fargesii* nuts decreased with increasing nut abundance. Jansen *et al.* (2004)

observed slower removal rates of *Carapa procera* nuts from seed stations in mast years but found that the extent of scatter hoarding was the same. Li & Zhang (2007) found that although masting reduced the removal rate of experimental *Prunus armeniaca* nuts, the number of nuts scatter hoarded by rodents increased. There have been some positive results. Yellow pine chipmunks and other small mammals removed and stored the wind-dispersed seeds of Jeffrey pine more rapidly in mast years than in non-mast years (Vander Wall 2002). This suggests that these rodents exhibit a functional response to the seeds, focusing their energies on removing the seeds when they are abundant.

Some of the apparent lack of support for the seed-dispersal hypothesis is because the results of some seed removal studies have been misinterpreted. Ideally, nuts used in removal studies should represent what is happening to the population of 'wild' nuts that have fallen to the ground and are being harvested by animals. As noted above, seed and nut removal rates in mast years often are found to be the same or slower than those found in non-mast years (e.g. Wastljung 1989; Jansen *et al.* 2004; Xiao & Zhang 2006). These results have been interpreted by some to mean that scatter-hoarding animals are not effective harvesters of nuts in mast years (e.g. Kelly & Sork 2002; Xiao *et al.* 2005b). However, I believe this interpretation to be incorrect. For example, if nuts are 10 times more abundant in a mast year than in a non-mast year and if removal of experimental nuts along a transect truly represents the rate of removal of the population of 'wild' nuts on the ground at large, then equal rates of removal of experimental nuts in mast and non-mast years would really mean that the number of nuts being removed is 10 times greater in the mast year. During the mast year, the population of experimental nuts is 'diluted' by the abundance of 'wild' nuts, so every time an experimental nut is removed, about 10 wild nuts also must have been removed. To interpret nut removal data properly in a multi-year study, one must know the relative sizes of the nut crops in each year of the study. I believe that inattention to this issue has led to a disparity between what appears to be relatively slow removal rates of experimental nuts in mast years and the large number of 'wild' nuts actually being stored.

Nut-caching animals, in fact, are well known for their nearly ceaseless activity removing and caching nuts from productive trees (Chettleburgh 1952; Ligon 1978; Darley-Hill & Johnson 1981; Hutchins & Lanner 1982; Tomback 1982; Johnson & Adkisson 1985; Steele & Koprowski 2001; Vander Wall 2002). Seed-caching animals (and other granivores) quickly recruit to productive trees in their home range (e.g. Chettleburgh 1952; Vander Wall 1988; Christensen & Whitham 1991; Jansen *et al.* 2004). During mast years, the number of nuts eaten at the source plant is usually small and the rest of the crop is stored, whereas in non-mast years virtually all of the crop is consumed with little if any being stored (Jensen 1985; Wastljung 1989; Vander Wall 1994a, 1997; Jansen *et al.* 2002, 2004; Xiao & Zhang 2006). As noted earlier, during periods of nut abundance, many seed-caching animals

store more nuts than they could possibly consume as a hedge against uncertainty. Filled nuts that fail to be scatter hoarded, on the other hand, rarely produce healthy seedlings (e.g. Jansen *et al.* 2004).

The different ways that food hoarders manage stored nuts during mast compared with non-mast years are also very important. In mast years, rates of cache pilferage are lower, animals handle nuts less often, there is less secondary caching (new caches made from nuts taken from an original cache) and nut survival is higher (Vander Wall 2002; Jansen *et al.* 2004). This is apparently because an individual stored nut has less value to animals during mast years. This change in caching dynamics during mast years is vitally important to the plant. Reduced secondary caching limits secondary dispersal (shorter primary-dispersal distance is also predicted in mast years because the value of individual nuts is lower; Moore *et al.* 2007; but see Vander Wall 2002; Li & Zhang 2007), but this limitation also benefits plants because if animals handle nuts less often there are fewer opportunities for animals to eat nuts. Less handling means potentially greater survival of the seeds.

And, indeed, masting increases fitness of nut-bearing trees (Watt 1923; Jensen 1985). For example, Jansen *et al.* (2004) reported a 4.5-fold increase in *per capita* *C. procera* seedling establishment in seed-rich years relative to seed-poor years. Jeffrey, sugar (*Pinus lambertiana*) and ponderosa (*P. ponderosa*) pines with simulated crops of seeds in synchrony with the local population of trees had more seeds survive to the time of germination during two springs (1998: ponderosa 8.9%, Jeffrey 2.1%, sugar 9.6%; 1999: ponderosa 8.3%, Jeffrey 8.2%, sugar 12.7%) compared with trees with simulated seed crops that were out of synchrony with the local population (2000: ponderosa 4.0%, Jeffrey 1.4%, sugar 1.4%; Vander Wall 2002). Jensen (1985) supplemented beechnuts at four sites (simulating mast crops) and found 30 per cent cache survival whereas all caches disappeared at control sites with no supplemental beechnuts. In other mast years, Vander Wall (2008) found an average of only 1.8 Jeffrey pine seedlings (from seeds initially dispersed by the wind) in fenced plots ($n = 8$) that excluded seed-caching rodents compared with an average of 110 seedlings in paired unfenced plots. These examples indicate that despite the fact that rodents eat seeds, they have a very positive impact on seedling establishment.

The seed-dispersal hypothesis for the evolution of masting is distinct from the predator satiation hypothesis for three reasons (although the two hypotheses are not mutually exclusive). First, scatter-hoarding mutualists (which are also seed predators) do not become satiated during the harvest phase of nut handling, at least not to the extent that animals that behave strictly as seed predators become satiated. However, during years of seed abundance, these same mutualists are likely to become satiated (predator satiation hypothesis) as they eat nuts during the cache recovery phase (e.g. winter). For scatter-hoarding animals, the predator satiation has its greatest effect *after* nut storage: because more nuts are cached than can be

consumed, many nuts escape predation (Jensen 1985). Second, scatter-hoarding animals do not simply ignore excess nuts as do satiated seed predators, they gather them and move them from a state (e.g. tree canopy or the ground surface) where successful germination is unlikely to a state (i.e. buried in soil) where they could produce healthy seedlings. Third, before storage, nuts are vulnerable to a wide variety of seed predators (e.g. insects, browsing ungulates, larder-hoarding rodents) but after storage the number of potential seed predators is much reduced (e.g. the hoarder and a few species that can pilfer caches) (Leaver & Daly 2001; Vander Wall & Jenkins 2003; Vander Wall *et al.* 2009). Burying nuts provides them with a certain degree of protection. It is much easier to satiate this reduced set of predators after nuts have been dispersed and stored. Thus, I argue that the predator satiation hypothesis is not a complete explanation for masting in nut-bearing plants; masting also benefits plants by increasing the proportion of nuts that are dispersed, by changing the way nuts are managed by food-hoarding animals and by decreasing access of those stored nuts to non-hoarding species (Christensen & Whitham 1991; Vander Wall 2002; Jansen *et al.* 2004).

5. SEED ODOUR

Once seeds and nuts are cached in soil, it is in the best interest of the plant to minimize removal of those propagules. Animals that scatter hoard food are known to retrieve that food using spatial memory (Vander Wall 1982, 1991; Kamil & Balda 1985; Jacobs & Liman 1991; Jacobs 1992a; Clayton & Krebs 1994; Pravosudov 2003), but rodents can also use olfaction to pilfer seeds (corvids appear to be incapable of finding cached seeds using olfaction). Therefore, one might predict that natural selection has acted on buried seeds and nuts to reduce their odour to a minimum (Janzen 1971); individual seeds with stronger odours are more likely to be located whereas those with weak odours might be overlooked by foragers. Although animals recache many of the seeds that they remove from caches, a decreased probability of discovery means a decreased probability of consumption.

Hollander *et al.* (submitted) tested this hypothesis by comparing the rate of removal of wildland seeds and cultivated seeds from caches. Cultivated seeds (i.e. sunflower, millet) have not been subject to intense natural selection regarding seed odours and, in fact, artificial selection might have acted, inadvertently, to increase seed odours above that present in ancestral populations. Wildland seeds that rodents frequently scatter hoard (i.e. Jeffrey pine, antelope bitterbrush (*Purshia tridentata*), Indian ricegrass (*Achnatherum hymenoides*)), on the other hand, presumably have been subject to intense selection for millions of years. In this comparison, sunflower seeds were removed from caches more rapidly by rodents than wildland seeds (Hollander *et al.* submitted). The result for millet was equivocal: at two sites, rodents removed millet faster than most wildland seeds and at one site slower than most wildland seeds. These

differences in rate of seed removal cannot be explained by differences in preferences, because the most preferred seeds (Jeffrey pine and Indian ricegrass seeds) were usually removed most slowly. Similar studies need to be conducted with a variety of other seed and nut types before broad conclusions can be reached, but the data suggest that wildland plants are under strong natural selection to minimize seed odours.

6. CONCLUSIONS

Plants that are dispersed by scatter-hoarding animals have evolved a number of strategies that increase the probability of successful seed dispersal. Plants should not be viewed as passive participants in these plant–animal interactions, depending on the imperfect foraging of scatter-hoarding animals to lose stored items in space and time. Plants not only produce seeds and nuts that are attractive to scatter hoarders, but other traits of those seeds and nuts and the way they are produced help to ensure that once those items are cached, there is a greater likelihood that they will escape consumption and establish seedlings.

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