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## Two-phase seed dispersal: linking the effects of frugivorous birds and seed-caching rodents

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**Abstract** Frugivorous birds disperse the seeds of many fruit-bearing plants, but the fate of seeds after defecation or regurgitation is often unknown. Some rodents gather and scatter hoard seeds, and some of these may be overlooked, germinate, and establish plants. We show that these two disparate modes of seed dispersal are linked in some plants. Rodents removed large (> 25 mg) seeds from simulated bird feces (pseudofeces) at rates of 8–50%/day and scatter hoarded them in soil. Ants (*Formica sibylla*) also harvested some seeds and carried them to their nests. Rodents carried seeds 2.5 ± 3.2 m to cache sites (maximum 12 m) and buried seeds at 8 ± 7 mm depth. Enclosure studies suggest that yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*) made the caches. In spring, some seeds germinated from rodent caches and established seedlings, but no seedlings established directly from pseudofeces. This form of two-phase seed dispersal is important because each phase offers different benefits to plants. Frugivory by birds permits relatively long-range dispersal and potential colonization of new sites, whereas rodent caching moves seeds from exposed, low-quality sites (bird feces on the ground surface) to a soil environment that may help maintain seed viability and promote successful seedling establishment.

**Keywords** Bird feces · Frugivory · Granivory · Scatter hoarding · Seed dispersal

### Introduction

Frugivory by birds coupled with elimination of seeds in feces is a well-known means of plant dispersal (Wenny and Levey 1998; Loiselle and Blake 1999; Herrera 2002), but postdispersal fate of seeds in bird feces has received little study (e.g., Herrera et al. 1994; Wang and Smith 2002). Fecal deposits are often unfavorable establishment sites for seedlings because seeds can be deposited on an inhospitable surface, exposed to seed predators, fungi, or harsh abiotic conditions (desiccation, variation in temperature, ultraviolet light, etc.; De Steven and Putz 1984; Sallabanks and Courtney 1992; Normah et al. 1997; Lambert 2002). Feces are often rich in seeds, so if germination occurs, competition can be intense (Howe 1989). Successful establishment of seedlings is often associated with the movement of seeds away from the point of deposition, either down into the soil or horizontally across the soil surface (Sheldon 1974; van Tooren 1988). It is generally assumed that successful seeds are those that avoid detection by animals (Janzen 1982a, b; LoGiudice and Ostfeld 2002; Moles et al. 2003) and get buried in soil or plant litter by abiotic processes (van Tooren 1988; Chambers et al. 1991).

In the tropics, animals are important secondary dispersers of seeds in feces. Ants remove seeds from bird feces and carry them to their nutrient-rich nests where some seeds germinate and establish plants (Roberts and Heithaus 1986; Davidson 1988; Kaufmann et al. 1991; Kaspari 1993; Levey and Byrne 1993; Bohning-Gaese et al. 1999; Passos and Oliveira 2002; Pizo et al. 2005). In recent years, dung beetles have been found to move mammal dung and its embedded seeds for short distances to nesting or feeding sites (Estrada and Coates-Estrada 1991; Andresen 2001, 2002). A portion of this dung is buried at a depth that permits seedling emergence and establishment. And rodents are known to remove seeds from mammal feces and scatter hoard them in soil (Forget and Milleron 1991; Wenny 1999; Feer and Forget 2002). These secondary seed movements often result

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in patterns of seedling recruitment that are quite different from the patterns of primary seed dispersal generated by frugivorous animals (Schupp 1995; Rey and Alcantara 2000).

In temperate ecosystems, secondary movement of seeds from feces has not received much attention. Those that have monitored seed removal often assume that removed seeds had been consumed (e.g., LoGiudice and Ostfeld 2002). We tested the idea that rodents in temperate forests secondarily disperse seeds initially ingested and dispersed by birds (primary dispersers).

Bird feces are amenable to experimental manipulation to follow the harvest and secondary movements of seeds. The feces of omnivorous, frugivorous birds, such as the American robin (*Turdus migratorius*), is a combination of partially digested food (often containing viable seeds) from the bird's digestive tract and nitrogenous wastes (primarily uric acid) from the urinary system (Singer 2003). These two components of feces merge in the cloaca before elimination. The uric acid forms a white precipitate that partially encloses the dark-colored material from the digestive tract. In this study, we created pseudofeces by placing seeds labeled with the radioisotope sandium-46 in a suspension of uric acid. The pseudofeces had an appearance and chemical composition similar to that of real bird feces, and the radioisotope permitted us to monitor the presence of seeds in feces and track seed movements away from fecal deposits.

We tested five hypotheses regarding the behavior of rodents that encounter bird feces that contain seeds. First, rodents remove seeds from bird feces. Second, rodents cache some of the seeds removed from bird feces (i.e., removed seeds are secondarily dispersed). Third, large seeds are more likely to be secondarily dispersed than smaller seeds. Fourth, white bird feces attract foraging rodents. And fifth, the rate of seed removal from feces is independent of the availability of alternative foods.

## Materials and methods

We conducted this study in the Whittell Forest, a facility of the University of Nevada System, in the Carson

Range  $\approx 30$  km south of Reno, NV (39°15'35"N, 119°52'35"W, 1,970 m). The main study site is a 0.25 ha plot of open Jeffrey pine (*Pinus jeffreyi*) with an understory of antelope bitterbrush (*Purshia tridentata*) on decomposed granitic soils. The climate is semiarid with hot, dry summers and winters with snow accumulations of  $\approx 1$  m.

We assumed that seed size would play an important role in determining whether rodents would remove seeds from feces, so we selected fruit with a broad range of seed sizes. We gathered the fruits of seven common plants that grow on the east slope of the Sierra Nevada that are eaten by songbirds (Table 1), and we extracted and cleaned the seeds. We labeled the seeds with scandium-46, a gamma-emitting radionuclide (half-life of 84.5 day) (Vander Wall 2000). In the field, we established 140 stations in a 10  $\times$  14 grid with 3-m spacing. Twenty stations were assigned to each seed species in a randomized block design. We created pseudofeces by placing seeds on  $\approx 0.5$  ml of uric acid (Sigma Chemical Inc.) suspension on the ground, and adding an additional 0.5 ml of uric acid to cover the seeds. Most seeds were totally obscured by the uric acid. Number of seeds per fecal deposit varied with seed size such that the mass of seeds per deposit was similar: *Prunus emarginatus* (2 seeds), *Rhamnus rubra* (2 seeds), *Cornus stolonifera* (3 seeds), *Amelanchier pallida* (4 seeds), *Rosa woodsii* (10 seeds), *Ribes nevadense* (20 seeds), *Sambucus cerulea* (20 seeds). The number of seeds per fecal deposit was probably within the range seen in the feces of wild, frugivorous birds, but sometimes large seeds (e.g., *Prunus*) are regurgitated rather than passed through the digestive tract. We established the grid on 15 August 2003 and checked it eight times at irregular intervals until 18 October. During each visit, we checked all pseudofeces and searched for caches using a Geiger counter on the grid and  $\approx 5$  m zone around the grid. On 2 and 19 May 2004, we resurveyed all fecal deposits and cache sites to locate emergent seedlings.

To determine whether uric acid influenced the foraging activity of rodents, we established a seed removal transect (Vander Wall 1994) of 100 stations (50 with uric acid pseudofeces alternating with 50 without uric acid) with 5-m spacing using *Rhamnus* seeds. We established the transect at a nearby site, monitored it over 3 days (31

**Table 1** Characteristics of fruits and seeds of seven species used in artificial bird feces

Species	Fruit traits				Seed mass (mg) (mean $\pm$ 1 SD)
	Color	Shape	Size (mm)	Number of seeds	
<i>Prunus emarginata</i> Bitter cherry	Red	Round	9–10	1	64.7 $\pm$ 22.9
<i>Rhamnus rubra</i> Sierra coffeeberry	Black	Round	9–11	2–3	55.5 $\pm$ 3.0
<i>Cornus stolonifera</i> American dogwood	White	Round	6–7	1	34.9 $\pm$ 3.6
<i>Amelanchier pallida</i> Pallid serviceberry	Purple	Round	9–11	1–4	28.3 $\pm$ 2.9
<i>Rosa woodsii</i> Wild rose	Red-orange	Ovoid	12 $\times$ 15	5–30	11.6 $\pm$ 1.5
<i>Ribes nevadense</i> Sierra currant	Bluish	Ovoid	7 $\times$ 10	10–13	2.3 $\pm$ 0.3
<i>Sambucus cerulea</i> Blue elderberry	Bluish	Round	5–6	3	2.1 $\pm$ 0.3

August–2 September 2003) and recorded seed removal. Three weeks later (20–22 September), we repeated the study in the midst of a large Jeffrey pine seed fall to test the effect of background seed density on the rate of seed removal from pseudofeces.

During July 2004, we tested the response of isolated yellow pine chipmunks (*Tamias amoenus*;  $n = 7$ ) and deer mice (*Peromyscus maniculatus*;  $n = 3$ ) to fecal deposits containing either *Rhamnus* or *Prunus* seeds inside 10×10 m rodent-proof enclosures. The enclosure had wire mesh walls  $\approx 70$  cm high topped with aluminum flashing. The wire mesh extended  $\approx 50$  cm into the ground to prevent rodents from burrowing in or out of the enclosure. We placed 16 pseudofeces containing two radioactive seeds (8 fecal deposits for each species) identical to those used in 2003 in a 4×4 grid with  $\approx 2$ -m spacing. After 24 h, we removed the rodent and surveyed the enclosure to locate cached and eaten seeds. We provided water but not food to rodents during trials.

We used survival analysis (Proc Lifereg in SAS, 2000, Allison 1995) to test for differences in the rates of removal of different species of seeds from pseudofeces. We used interval censoring and a Weibull distribution (Allison 1995). We used fecal deposits (not seeds) as the response variable, and required that at least half of the seeds be taken from a deposit before considering that fecal deposit to be depleted by animals.

## Results

Rodents removed the four largest ( $> 25$  mg; Table 1) seed species from bird pseudofeces (Fig. 1). *Rhamnus* seeds disappeared the fastest (50.0%/day) while the three other large-seeded species were removed at rates between 8.2%/day and 11.7%/day. Survival analysis showed that rodents removed *Rhamnus* seeds 6.9 times faster than *Prunus* seeds ( $\chi^2 = 35.82$ ,  $P < 0.0001$ ) and

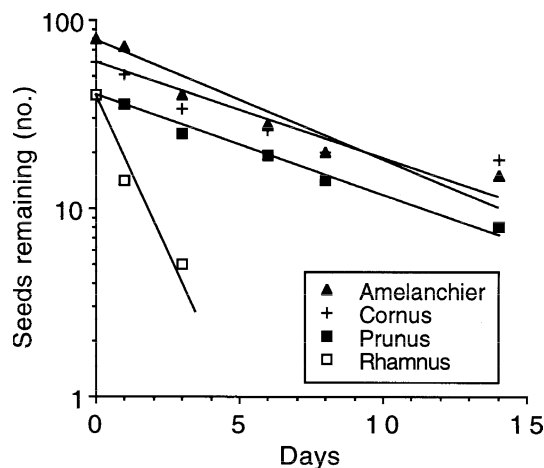


Fig. 1 Seeds remaining of four plant species (*Amelanchier*, *Cornus*, *Prunus*, and *Rhamnus*) in bird pseudofeces after rodent and ant foraging. Note the log scale on the y-axis

that rodents removed *Amelanchier* seeds 1.9 times faster than *Cornus* seeds ( $\chi^2 = 6.64$ ,  $P < 0.01$ ). *Prunus* seeds disappeared at rates similar to *Cornus* and *Amelanchier* seeds ( $P > 0.25$  for both comparisons). The three smallest species of seeds ( $< 12$  mg; Table 1) were not gathered from pseudofeces by rodents, but rodents appeared to have examined  $> 60\%$  of pseudofeces containing these small seeds.

Seeds within pseudofeces were not always taken at the same time. *Prunus* stones in a fecal deposit were taken during different visits at least 54.3% of the time. The percentages for *Cornus*, *Rhamnus*, and *Amelanchier* were at least 41.3%, 30.0%, and 8.1%, respectively. This suggests that rodents made repeated visits to fecal deposits to find seeds.

We found 38 rodent caches containing 52 seeds (1.4 seeds/cache), accounting for 27.1% of the 192 large seeds taken from feces. Caches were  $2.5 \pm 3.2$  m (mean  $\pm 1$  SD) away from the nearest fecal deposit of that seed species (minimum secondary dispersal distances; Fig. 2). Burial depths were  $7.8 \pm 7.0$  mm (range = 1–40 mm), probably within the range of depths suitable for germination and emergence. We found 14 *Prunus* caches (48.6% of seeds taken from feces), eight *Rhamnus* caches (22.5%), 13 *Cornus* caches (44.4%) and three *Amelanchier* caches (9.6%).

To determine which species of rodents were making caches, we offered *Prunus* and *Rhamnus* seeds embedded in pseudofeces to yellow pine chipmunks and deer mice isolated in field enclosures. One chipmunk and two mice removed seeds from pseudofeces during these short trials. The chipmunk made two *Prunus* and three *Rhamnus* caches, and the two deer mice made four *Prunus* and four *Rhamnus* caches. These caches were similar to those made in the field experiment where rodents had free access to pseudofeces.

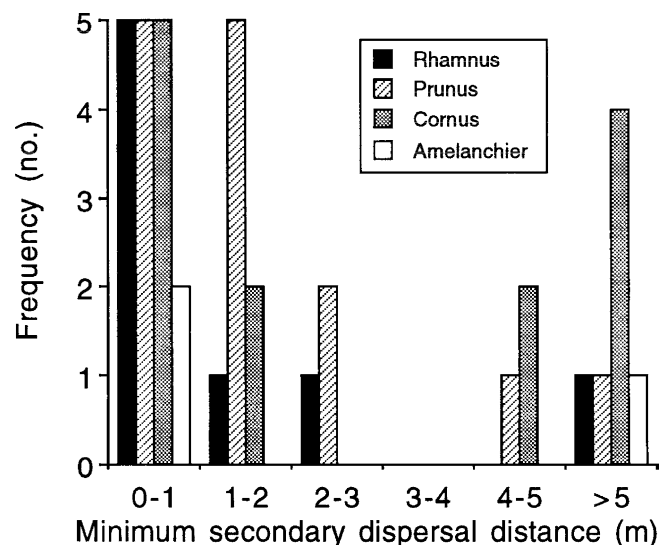


Fig. 2 The minimum distances that rodents (as secondary dispersers) transported seeds of four plant species to cache sites

Ants (*Formica sibylla*) removed seeds from at least 14 fecal deposits. Seeds taken by ants included eight *Rhamnus* and several of the smaller species: two *Amelanchier*, six *Rosa*, and two *Sambucus*. Most of these seeds were carried deep into ant nests, but one *Sambucus* and two *Amelanchier* seeds were found discarded and partially buried just outside nests. None of them successfully germinated the following spring.

Autumn rains eroded pseudofeces and exposed small seeds. Some of the *Rosa* (31 seeds; 15.5% of those in feces), *Ribes* (29 seeds, 7.3%), and *Sambucus* (12 seeds; 3.0%) seeds were scattered up to 10 cm (mean  $\pm$  1 SD = 2.1  $\pm$  1.5 cm) from the fecal deposit by rain drops. Soil disturbances (e.g., digging by rodents) near 33 of 60 fecal deposits with small seeds further scattered seeds and partially buried seeds and feces. By spring, we could not relocate any of these seeds, suggesting that they had become buried, eaten by seed predators, or dispersed farther away from the pseudofeces.

Uric acid precipitate in bird feces is conspicuous and may act as a signal of potential seed availability to foraging rodents. Alternatively, uric acid is a mild irritant and may deter foraging rodents. We tested for these effects along transects using *Rhamnus* seeds with and without pseudofeces. Animals removed *Rhamnus* seeds on the ground (without pseudofeces) at a rate similar to seeds in pseudofeces (51%/day vs. 54%/day, respectively;  $X^2 = 1.82$ ,  $P = 0.117$ ), indicating that the uric acid neither discourages nor attracts foragers.

Availability of alternative foods did not influence rate of removal of seeds from pseudofeces. Rodents removed *Rhamnus* seeds from pseudofeces at a similar rate (61%/day vs. 54%/day, respectively;  $X^2 = 0.18$ ,  $P = 0.671$ ) whether or not there was a rich supply of highly preferred Jeffrey pine (*Pinus jeffreyi*) seeds (Vander Wall 1995) available. This suggests that animals do not resort to removing seeds from feces only when other foods are unavailable.

By spring, most uric acid had dissolved and pseudofeces were difficult to distinguish. Among the 60 fecal deposits that contained seeds in autumn, only one produced a single *Sambucus* seedling, which died within several days. However, three *Rhamnus* caches (37.5%) produced germinants. In addition, 15 caches (39%; seven *Prunus* caches, six *Cornus* caches and two *Rhamnus* caches) contained dormant, apparently viable seeds.

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## Discussion

Rodents removed relatively large seeds (> 25 mg) from simulated bird feces quickly, and they cached many of those seeds in soil. Using field enclosures, we demonstrated that yellow pine chipmunks and deer mice remove seeds from pseudofeces and cache them in a manner similar to that observed in the field experiment. Furthermore, the caches that rodents made in the field experiment were similar to those made by yellow pine chipmunks and deer mice in earlier studies (Vander Wall

2000; Vander Wall et al. 2001). Because these and related species of *Tamias* and *Peromyscus* are common throughout a large portion of temperate North America, we suspect that this interaction between frugivorous birds and seed-caching rodents is probably far more common than currently appreciated.

Similar patterns of seed removal have been found in other studies. Kollmann et al. (1998) monitored the removal of 12 seed species from Petri dishes by rodents in Germany and southern England and found that *Prunus* spp. seeds disappeared faster than *Cornus sanguinea* and *Rosa fruticosus* seeds, and that *Sambucus nigra* seeds were among the species with the slowest removal rates. However, they assumed that the removed seed had been consumed even though the larger seeds (*Prunus* and *Cornus*) might have been scatter-hoarded.

Many birds regurgitate or spit out large seeds rather than pass them through their digestive tract (Meyer and Witmer 1998; Witmer 1998). Our result from the seed removal transects reveals that the rate of removal of seeds in pseudofeces is not different from the seeds unassociated with uric acid, suggesting that seeds regurgitated by birds are likely to be removed from the ground surface just as quickly as those that are defecated by birds. Feer and Forget (2002) also found that mammal feces did not influence the rate of seed removal by rodents.

Rodents ignored small species of seeds. Abiotic factors (rain and wind) moved *Rosa*, *Ribes*, and *Sambucus* seeds a few centimeters across the ground. In addition, animals inadvertently disturbed the ground near pseudofeces, causing burial of many seeds. Sheldon (1974) and van Tooren (1988) have made similar observations. Ants moved some of the smaller seeds short distances, but we did not collect sufficient data to determine whether they might have a positive impact on seedling recruitment.

In this study, recruitment was poor for all seed species whether or not they were removed from pseudofeces by animals. One reason for this was that our study plot was a poor habitat for five of the seven plant species tested (only *Rosa woodsii* grew on our study plot and *Rhamnus rubra* occurred in similar habitat). The other five plant species occur in more mesic habitats in shaded lodgepole pine forests or along riparian corridors. If we had conducted our study in a more mesic habitat, we probably would have had more seeds germinate from pseudofeces and rodent caches.

This study demonstrates that some of the larger seeds in bird feces can experience two distinct phases of seed dispersal (i.e., diplochory). Each of these phases can offer different benefits to plants (Vander Wall and Longland 2004). Phase one or primary dispersal by frugivorous birds has the potential to colonize new areas (Willson 1993; Gibson and Wheelwright 1995) and helps seeds escape potentially high density-dependent seed mortality near the parent plant (Janzen 1970). Birds typically damage or destroy only a small fraction of the seeds they ingest, and passage of the seeds through the

bird's digestive tract can facilitate germination (Yagihashi et al. 1998; Traveset et al. 2001). However, seeds are deposited on the ground surface where they are vulnerable to postdispersal seed predators, extreme physical conditions, and where germination failure can be high. Rodents are important postdispersal predators of seeds, but they also scatter hoard many seeds (phase-two dispersal). Caching by rodents does not move seeds far relative to that achieved by bird dispersal, so the colonization of new patches is unlikely to be an important benefit of phase-two dispersal. However, caching places seeds in conditions that often favor seedling establishment. Once cached, seeds are relatively safe from other sources of seed mortality such as ants, beetles, and birds that act as seed predators. Two-phase seed dispersal has the potential to increase the overall effectiveness of seed dispersal over any single means of seed dispersal (Vander Wall and Longland 2004).

A measure of the complexity of ecological communities is the nature and frequency of species interactions. The two-phase seed dispersal syndrome described here is a novel form of species interaction that will probably prove to be more common in temperate regions than currently recognized, and, once identified and understood, these species interactions are likely to help explain the patterns of species diversity and how species persist in nature. For example, realizing that some plant propagules are dispersed in two or more discrete phases may help us understand how seeds survive and produce seedlings once they reach a suitable habitat. A deeper appreciation of complex seed dispersal systems will help us understand better the functioning of ecological communities and the selective forces (e.g., how differing selection by primary dispersers, secondary dispersers, and the abiotic environment interact to influence the evolution of seed size) acting on fruit and seed characteristics.

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