# Dispersal of an herbaceous perennial, *Paeonia brownii*, by scatter-hoarding rodents[1]

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*Abstract*: Most plants that are dispersed by seed-caching animals are large, woody trees that produce large, nutritious nuts. But a few species dispersed in this way are relatively small shrubs or perennial herbs. Wild peony (*Paeonia brownii*) is a perennial herb in western North America that is dispersed by seed-caching rodents such as chipmunks (*Tamias* sp.), deer mice (*Peromyscus maniculatus*), and pocket mice (*Perognathus parvus*). These rodents harvest seeds from the dehiscent, pendant pods and transport them short distances (most <20 m) and cache 1 or a few seeds from 0 to 15 mm deep in soil. Unrecovered seeds germinate in the spring. Unlike most nuts, peony seeds are not highly preferred food items; they are rich in carbohydrates and low in lipids and protein. Rodents remove peony seeds slowly compared to Jeffrey pine (*Pinus jeffreyi*) seeds, which are highly preferred by rodents and dispersed in the same manner. The low preference for peony seeds may benefit the plants: peony seeds are slow to be harvested and cached, but also slow to be removed from caches and eaten. Small herbaceous plants cannot produce large crops of large, attractive seeds to satiate potential seed dispersers, as do most nut-bearing trees, so producing low-preference food items probably helps these types of plants to ensure that some of the seeds survive to germinate.
*Keywords*: caching, food hoarding, granivory, mutualism, *Paeonia brownii*, perennial herbs, scatter hoarding.

*Résumé* : La plupart des végétaux dont les graines sont dispersées par des animaux qui font des réserves sont de grands arbres qui produisent de grosses noix nutritives, mais quelques espèces d'arbustes relativement petits ou de plantes herbacées vivaces sont également dans ce groupe. La pivoine sauvage (*Paeonia brownii*) est une herbacée vivace de l'ouest de l'Amérique du Nord dont les graines sont dispersées par des rongeurs comme les tamias (*Tamias* sp.), la souris sylvestre (*Peromyscus maniculatus*) et la souris à abajoues des pinèdes (*Perognathus parvus*). Ces rongeurs récoltent les graines des gousses déhiscentes qui pendent et les transport sur de courtes distances (pour la plupart <20 m) puis enterrent une ou quelques graines entre 0 et 15 mm de profondeur. Les graines qui n'ont pas été récupérées germent au printemps. À la différence de la plupart des noix, les graines de pivoine ne sont pas un aliment préféré des rongeurs; elles sont riches en glucides et pauvres en lipides et en protéines. Les rongeurs récoltent les graines de pivoine à un rythme peu soutenu en comparaison à celles du pin de Jeffrey (*Pinus jeffreyi*) qui elles sont grandement appréciées des rongeurs qui les dispersent de la même manière. Le fait que les graines de pivoine soient peu préférées des rongeurs peut être bénéfique pour la plante : les graines tardent à être récoltées et enfouies, mais tardent aussi à être récupérées ensuite pour être mangées. Les plantes herbacées de petite taille ne peuvent pas produire de grandes quantités de grosses graines attirantes et rassasiantes pour les agents de dispersion potentiels, comme le font la plupart des arbres à noix, donc la production d'un aliment peu préféré contribue probablement à assurer que certaines des graines de ces plantes vont survivre et germer.
*Mots-clés* : cache, entreposage dispersé de réserves, granivorie, mutualisme, *Paeonia brownii,* plantes herbacées vivaces, réserves de nourriture.

Nomenclature: Hickman, 1993; Wilson & Reeder, 2005.

## Introduction

Dispersal of most plant seeds falls into one of 7 or 8 seed dispersal syndromes (*e.g.*, by wind, ants, frugivorous animals, scatter-hoarding animals, etc.). Most of these syndromes have been recognized for centuries (Ridley, 1930; van der Pijl, 1982; Thanos, 1994) and have been well characterized. Seed dispersal by scatter-hoarding animals, for example, fits a well-prescribed format. Rodents, corvids, and a few other taxa harvest the seeds of plants and bury them in the ground as a future food source, and some of the propagules escape detection and later germinate,

establishing a new plant at a new site. Plants that have this mode of dispersal are usually dominant members of the plant community (*i.e.*, large trees) that produce large, nutritious propagules (*e.g.*, nuts) that are often poorly defended chemically (Vander Wall, 2010). Nut crops show great interannual variation in size and are often synchronized over large geographic areas (*i.e.*, mast seeding) to satiate potential seed predators (Kelly, 1994; Koenig *et al.*, 1994; Kelly & Sork, 2002) and to increase the efficiency of seed dispersal (Vander Wall, 2002; Jansen, Bongers & Hemerik, 2004). Examples of such species are oaks (*Quercus*), hickories (*Carya*), walnuts (*Juglans*), beech (*Fagus*), and chestnut (*Castanea*) of the eastern deciduous forest (Stapanian & Smith, 1978; Sork, 1983; Johnson & Adkisson, 1985; Steele *et al.*, 1993), Brazil nuts (*Bertholletia excelsa*),

palms (*e.g.*, *Astrocaryun paramaca*), and carapa (*Carapa procera*) of tropical forests (Forget, 1991; Peres & Baider, 1997; Jansen, Bongers & Hemerik, 2004), and piñon, white-bark, and Jeffrey pines (*Pinus*) in coniferous forest of western North America (Vander Wall & Balda, 1977; Tomback, 1978; Vander Wall, 2002; 2008).

Not all plant species with propagules dispersed by scatter-hoarding animals fall neatly into this characterization. Hazels of eastern forests are not dominant trees but understory shrubs that spread vegetatively and can live to be hundreds of years old (Mehlenbacher, 1991); Indian ricegrass (*Achnatherum hymenoides*), antelope bitterbrush (*Purshia tridentata*), and green *Ephedra* (*Ephedra viridis*) are grasses and shrubs of our western rangelands (Vander Wall, 1994b; Longland *et al.*, 2001; Hollander & Vander Wall, 2009); and Joshua tree (*Yucca brevifolia*) is an arborescent yucca of the Mojave Desert (Vander Wall *et al.*, 2006; Waitman, Vander Wall & Esque, 2012).

Scatter-hoarding animals have seldom been documented dispersing herbaceous plants. Most herbaceous perennial plants differ from the species described in the above paragraphs in that they have relatively small (1–10 mg) seeds only a small fraction of the size of most nuts, most do not mast seed but tend to produce moderate-sized seed crops in most years, and they often produce seeds that remain dormant in the soil for many years. These plants are dispersed in a variety of ways, including wind, frugivory, burrs that hitch a ride on mammals, and ballistic projection. In recent years, a few perennial herbaceous plant species have been identified that are dispersed by scatter-hoarding rodents. For example, manroot (*Marah macrocarpa*), a member of the cucumber family (Cucurbitaceae), produces small dehiscent fruits that contain a single large seed following fire that are scatter-hoarded by rodents and jays (Borchert, 2004). There are a small number of herbaceous perennial plant species that are dispersed by scatter-hoarding rodents, but the dispersal syndrome of most of these plants has gone unrecognized and has not been investigated. One reason for this oversight is that these plants do not fit the syndrome that we expect from plant species that are dispersed by scatter-hoarding animals. Yet, a full understanding of this seed-dispersal syndrome cannot come until we appreciate the full range of plant characteristics and fruit and seed morphologies exhibited.

Wild peony (*Paeonia brownii*) is an herbaceous perennial that does not share many traits with nut-bearing trees yet appears to be dispersed by scatter-hoarding rodents (see next section). Here we reveal the nature of this plant–animal interaction through a series of experiments and studies and explore some of the differences and similarities with other plants dispersed in this way. In so doing, we hope to broaden our understanding of the characteristics and evolution of this seed dispersal syndrome.

### PEONIES

Peonies (Paeoniaceae: *Paeonia*) are native to the Northern Hemisphere and occur in 5 discontinuous areas: eastern Asia, central Asia, the western Himalayas, the Mediterranean region, and western North America. The southernmost species, *P. mascula atlantica*, occurs in northwest Africa (35°N), and the northernmost limit of the genus is near the Arctic Circle on the Kola Peninsula of Russia (67°N), where *P. lactiflora* can be found. Most peonies grow in areas that have temperate to cold climates and year-round precipitation (Halda & Waddick, 2004).

The genus *Paeonia* includes about 35 species of woody shrubs and perennial herbs with large, fleshy roots. Woody species, often referred to as tree peonies, can grow up to 3 m tall. Herbaceous forms usually have stems <1 m tall. Flowers range from 3 to 20 cm in diameter, and their colours vary from white to pink, crimson, purple, orange, and yellow.

*Paeonia brownii* and *P. californica* are the only species that occur in North America and are the sole members of the subgenus Onaepia. Some have suggested that *P. californica* is a subspecies of *P. brownii* (Sang, Crawford & Stuessy, 1997; Halda & Waddick, 2004), with the differences between the taxa supposedly due to ecological factors; *P. brownii* is xerophylic and *P. californica* is adapted to warmer, wetter climates (Stebbins, 1938). However, phylogenetic analysis shows that these species are genetically very different despite their morphological similarities (Sang, Crawford & Stuessy, 1997). *Paeonia brownii* is found at mid- to high elevations (200–3000 m) and typically grows in a mediterranean climate. It is also the more widespread of the 2 North American species, occurring from British Columbia to Montana and south from southern California to Utah. In western Nevada, *P. brownii* is sparsely distributed from Great Basin Desert scrub (about 1375 m elevation) to the Jeffrey pine (*Pinus jeffreyi*) forests (up to about 2000 m) in the Carson Range.

Both North American species are herbaceous. *Paeonia brownii* stems are up to 50 cm tall. Flowering takes place from April to June. The flowers are 2–3 cm wide, with broad, oval, maroon petals. Each flower produces up to 5 glabrous follicles that ripen from early July to mid August depending on elevation and climate. The relatively large seeds of *P. brownii* (approximately 11 mm in length; mean fresh mass [± 1 SE] 384 ± 9 mg) and the occasional observation of several seedlings growing in a clump, apparently from an animal cache, suggested that this species might be dispersed by scatter-hoarding rodents.

*Paeonia brownii* often grows in association with Jeffrey pine. Jeffrey pine seeds are similar in size to peony seeds and become available to seed dispersers at the same time as *P. brownii* seeds. Jeffrey pine seeds are also eagerly sought after by seed-caching rodents that disperse many seeds (*e.g.*, Vander Wall, 2008). Preliminary studies indicated that *P. brownii* seeds are often neglected, suggesting that they may be a relatively low preference food item. This suggests that *P. brownii* may be at a disadvantage when competing with Jeffrey pine for dispersal by scatter-hoarding rodents. There is little known about the natural history and ecology of *P. brownii*; hence, there are many potential questions regarding its ability to persist under the aforementioned conditions. First, do rodents disperse *P. brownii* seeds by scatter-hoarding them in soil, and, if so, what rodent species do so? Second, what traits of *P. brownii*

promote rodent seed dispersal? Third, what are the characteristics of *P. brownii* caches? Fourth, what microsites encourage *P. brownii* seed germination and emergence? And fifth, how does *P. brownii* fare in the competition for seed dispersers with Jeffrey pine?

## Methods

STUDY SITE

We made observations at 3 locations in western Nevada. The primary site was located in the Whittell Forest and Wildlife Area in Little Valley, located approximatively 30 km south of Reno, Washoe County, Nevada (39°14'49"N, 119°52'38"W, elev. 1975 m). Here, *Paeonia brownii* inhabits the ecotone between the lodgepole pine (*Pinus contorta*) forests on the valley bottom, with heavy, poorly drained soils, and Jeffrey pine forests on the slopes, with well-drained soils. Associated understory plants include antelope bitterbrush (*Purshia tridentata*), greenleaf manzanita (*Arctostaphylos patula*), and mule's ears (*Wyethia mollis*). We studied *P. brownii* at this site from summer 2009 to fall 2010.

Our second site was the Waterfall Fire site, located about 4 km west of Carson City, Carson City County, Nevada (39°11'06"N, 119°48'09"W, elev. 1570 m), about 9 km south of the Little Valley site and on the east slope of the Carson Range. This site experienced an intense wildfire on July 14, 2004 that burned 3565 ha. Peony plants at this site are robust, apparently because of the recent fire. Vegetation at the site is dominated by sagebrush (*Artemisia tridentata*) and antelope bitterbrush with sapling Jeffrey pines. Soils are similar to those at Little Valley. At this site, we studied *P. brownii* seed dispersal and seedling establishment in summer 2009 and spring 2010.

The third site was Red Rock, located approximatively 35 km north of Reno, Washoe County, Nevada (39°48'N, 119°56'W, elev. 1685 m). This is a Great Basin Desert site near the lower edge of the *P. brownii* elevation range. The soil type at the site is predominantly coarse, sandy loam, and the associated shrub community in this area consists of sagebrush (*A. tridentata*), rabbitbrush (*Chrysothamnus* sp.), lupine (*Lupinus* sp.), and desert peach (*Prunus andersonii*). This area experienced a wildfire on July 15, 2009 that burned 1255 ha. We studied the dispersal of *P. brownii* at this site during the summer and autumn of 2010.

IDENTIFYING POTENTIAL RODENT SEED CONSUMERS
AND DISPERSERS

We trapped rodents at all 3 sites in the autumn of 2009 and 2010 to determine the identity of all potential rodent seed consumers and dispersers. Trapping grids consisted of 40 Sherman live traps baited with sunflower seeds in a 4 × 10 array with 12 m between traps. The traps were open for 5 days and 5 nights and checked 2 times each day, in the late morning and late afternoon. We recorded species, sex, weight, and recapture information for each rodent caught, and marked each new capture with a numbered ear tag. The number of individuals of each species captured (the minimum population size) was used to characterize the rodent community composition at each site.

SEED PRODUCTION AND HARVEST

To estimate seed production, we counted the number of flowers per plant and carpels (immature pods) per flower for each of 5 flowers from each of 30 mature study plants (selected arbitrarily) at each site. We also measured the size of peony plants (greatest diameter, least diameter, and height) as a potential covariate of seed production. As the pods began to dehisce in late July, we counted the number of ripe seeds per pod for flowers on the 30 study plants. We used the mature seeds from these plants to determine seed mass. The nutrient content and presence of secondary compounds found in *P. brownii* seeds (with seed coats removed) were determined by Ward Laboratories, Inc. (Kearney, Nebraska, USA) in 2009 from the combined samples of 120 seeds from the 60 study plants of *P. brownii* in Little Valley and the Waterfall Fire site. We also determined the nutrient content of an equal number of Jeffrey pine seeds from numerous (>20) trees in Little Valley. We monitored these same peony plants for herbivory of flowers, pods, and foliage as the seeds developed.

To estimate the rate of seeds harvested by animals from plants, we placed ripe seeds under 30 *P. brownii* plants at each site in 13- × 13- × 1-cm trays made of 6 mm hardware cloth after fruits began to dehisce. We used trays to prevent loss of seeds in plant litter. Each tray contained 10 *P. brownii* seeds. Trays with seeds were deployed on August 15 in 2009 and on August 21 in 2010. We monitored the trays every day for the first 3 d and then weekly thereafter until most seeds were gone in both 2009 (Little Valley and Waterfall Fire sites) and 2010 (Little Valley and Red Rock sites).

SEED CACHING

We placed 50 seeds labelled with scandium-46 under each of 9 peony plants at Little Valley in 2009 and 10 peony plants in Little Valley in 2010 at the time that these peony plants were shedding their seeds (generally late August). We also conducted 6 trials at the Red Rock site in August 2010. We stationed video cameras (BirdCam 2.0, Wingscapes, Alabaster, Alabama, USA) near 5 of these plants to determine what type of animal removed the seeds. Seeds from 13 of these 25 trials were removed within 1 week so we deemed them successful.

After seeds were removed, we used a portable Geiger counter (Eberline ASP-1 meter and SPA-3 probe; ThermoFisher Scientific, Santa Fe, New Mexico, USA) to find cache locations. After excavating a cache, we wrote a unique number on the seeds with metallic ink, recorded the location and depth of the seed, and returned the seeds to the cache sites. The number on the seed helped us to track seeds that rodents excavated and recached and to differentiate previously unlocated caches from recached seeds. We avoided touching the experimental seeds and the ground within 50 cm of the cache site with our hands to prevent human odour from contaminating the seeds and the cache sites in order to keep rodents from using this cue to find buried seeds (Duncan *et al.*, 2002). We monitored all caches during the fall and checked them during the spring for seedlings.

CACHE PILFERING AND SEED PREFERENCE

To determine the rate of cache pilferage, we established 9 transects in the vicinity of the rodent trapping grids consisting of a total of 75 artificial caches of 3 different treatment types (25 caches per treatment). Treatment types alternated in a regular fashion as follows: 4 *P. brownii*, 4 Jeffrey pine, and 2 *P. brownii* and 2 Jeffrey pine seeds (mixed seed caches such as these are not uncommon in the wild). Jeffrey pine seeds, which are similar in size to those of *P. brownii*, were used as a reference species in this experiment because the removal rates are known for this seed type (Vander Wall, 1994a; 2008) and it is a preferred food of scatter-hoarding rodents (Vander Wall, 1995b). Mixed caches enabled us to compare rates of detection and seed preferences more directly. Each cache was 3 cm deep, within the range of depths that chipmunks bury seeds. We spaced caches about 5 m apart. We marked each cache using natural objects (*e.g.*, a combination of rocks, sticks, and pine cones) to prevent animals from learning cache markers. We monitored transects every day for the first 3 d and once a week thereafter.

In Little Valley, we established 3 transects in early September 2009 and 2 transects in 2010. We established 2 transects at the Waterfall Fire site in 2009 and 2 transects at the Red Rock site in 2010. We calculated the number of caches removed per day for each species. Caches where seeds were excavated but left on the surface were considered detected but not removed. Caches were considered removed when 2 or more seeds were taken. We used Program R Version 2.12.2 (R Development Core Team, 2011) with the survival package (Therneau and Lumley, 2011) to perform survival analysis with interval censoring and a Weibull distribution for comparison of seed removal rates from the seed cache transects.

SEED GERMINATION

We examined the effects of burial depth on the germination success of *P. brownii* using rodent-proof exclosures established in Little Valley in autumn 2008 and both Little Valley and the Waterfall Fire site in autumn 2009. Neglected seeds dry out and shrivel, so we hypothesized that dry *P. brownii* seeds would have lower germination success than fresh *P. brownii* seeds. *Paeonia brownii* seeds were characterized as dry if they were present on the ground for at least 2 weeks after falling out of a dehiscent pod and fresh if we removed them directly from a dehiscent pod at maturity, placed them in a sealed plastic bag, and stored them in a refrigerator until planting. Planting exclosures measured 1 × 2 m. In 2008, caches containing either a single, air-dried *P. brownii* seed, fresh *P. brownii* seed, or a Jeffrey pine seed were made on November 8 at 5 mm depth. A total of 133 caches were made in each enclosure, containing 30 dry peony seeds, 50 fresh peony seeds, 50 Jeffrey pine seeds, and 3 empty spots, haphazardly arranged in a 7 × 19 array. In 2009, caches containing a single seed were planted on October 6 at three depths (surface, 5 mm, 10 mm) and using 3 seed types (air-dried *P. brownii*, fresh *P. brownii*, Jeffrey pine).

We arranged these caches in 3 blocks each with 3 caches for each of the 3 seed types and depths and one blank spot, for a total of 84 sites in a 7 × 2 array. The seed type-depth treatment combinations were assigned at random within each block in each exclosure. Results of the 2008 planting were gathered in June 2009, and results of the 2009 planting were collected in June 2010 and April 2011. The 2008 planting data were analyzed using logistic regression with seed type and sub-site as main effects. The 2009 planting data were analyzed using logistic regression with depth and seed type as fixed effects and block, sub-site, and site as random effects.

## Results

SEED PRODUCTION

The plants were significantly larger at the Waterfall Fire site than in Little Valley ($F_{1, 58}$ = 50.16, $P < 0.001$). The number of flowers on plants was positively correlated with plant size at both sites but only significant at Little Valley (Waterfall Fire, $r = 0.215$, df = 28, $P > 0.1$; Little Valley, $r = 0.887$, df = 28, $P < 0.01$). There was no significant difference in the number of pods per flower at the 2 sites ($F_{1, 225}$ = 0.86, $P = 0.355$). However, pods of comparable size contained significantly more seeds on the plants in Little Valley ($F_{1, 18}$ = 9.35, $P < 0.001$). The average plant in Little Valley produced 4.5 ± 0.6 flowers with 2.7 ± 0.1 pods per flower and 8.0 ± 1.1 seeds per pod (about 97 seeds per plant), whereas the average plant at the Waterfall Fire site produced 19.7 ± 1.7 flowers with 2.9 ± 0.1 pods per flower and 5.5 ± 0.6 seeds per pod (approximatively 314 seeds/plant). Herbivory of pods was much higher in Little Valley, whereas desiccation caused many pods to abort at the Waterfall Fire site (Figure 1).

Nutritional analysis of seeds indicated that peony and Jeffrey pine seeds are significantly different ($X^2 = 18.539$, df = 2, $P < 0.001$). *Paeonia brownii* seeds are rich in carbohydrates compared to Jeffrey pine seeds, whereas the latter are rich in lipids and protein (Figure 2).

RODENT SEED CONSUMERS AND DISPERSERS

Potential rodent consumers of seeds at the Little Valley site, revealed by rodent trapping, were (in order of abundance) yellow pine chipmunks (*Tamias amoenus*), deer mice (*Peromyscus maniculatus*), golden-mantled ground squirrels (*Spermophilus lateralis*), and long-eared chipmunks (*T. quadrimaculatus*) (Table I). At the Waterfall
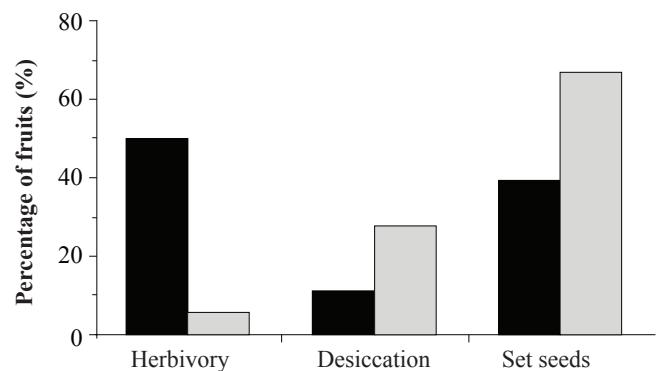


FIGURE 1. Fate of seed pods at the Little Valley (black) and Waterfall Fire (grey) sites in 2009. Herbivory included consumption of pods by insects, rodents, and deer. Some pods desiccate before producing mature seeds. Fully developed pods "set seeds" that are available for dispersal.

Fire site we caught deer mice, Panamint kangaroo rats (*Dipodomys panamintus*), and Great Basin pocket mice (*Perognathus parvus*), and at Red Rock, Great Basin pocket mice (*Perognathus parvus*), Panamint kangaroo rats, deer mice, antelope ground squirrels (*Ammospermophilus leucurus*), little pocket mice (*P. longimembris*), and Ord's kangaroo rats (*D. ordii*). We also recorded chipmunks and golden-mantled ground squirrels eating and carrying peony seeds in their cheek pouches at video stations.

SEED HARVEST

Rodents removed seeds from wire-mesh trays under peony plants (Figure 3) at an average rate of 5.1% and 6.9% per day at the Little Valley and Waterfall Fire sites in 2009, respectively. In 2010, rodents removed seeds at an average rate of 0.77% and 6.2% per day at the Little Valley and Red Rock sites, respectively.

SEED CACHING

In the radio-labelled seed study in Little Valley, we located 72 caches in 2009, with a mean dispersal distance of $6.5 \pm 4.4$ m (range = 0.5–19.4 m), a mean depth of $7.6 \pm 9.9$ mm (range = 0–55 mm), and a median of 1 seed per cache (range = 1–7). We also located 1 larder that contained 32 seeds buried 50 cm deep in a deer mouse burrow. In 2010, we recorded 30 caches, with a mean dispersal distance of $4.4 \pm 3.2$ m (range = 0.3–11.8 m), a mean depth of $3.1 \pm 1.8$ mm (range = 1–6 mm), and a median of 2 seeds per cache (range = 1–5). Figure 4 summarizes caching

depth and distance from the source, and Table II describes caches at each of the trials performed in 2009 and 2010. We often found caches to be clumped. We attempted to track seeds at the Red Rock site using scandium-46, but we found only 1 cache at 1 site that contained all 50 seeds buried only 3 mm deep under a small lupine (*Lupinus* sp.).

Three caches made during the 2009 seed-caching trials were still present in spring 2010 and produced 8 seedlings (1.8% of the seeds we offered rodents and 6.5% of those that we found in caches), including a 7-seed cache that produced 6 seedlings.

CACHE PILFERING

The rate of discovery of seed caches was significantly different between sites in 2009 ($Z = 6.69$, $P < 0.001$). In 2009, the detection and removal of peony caches was much faster at Little Valley than at the Waterfall Fire site (detection: $Z = 2.87$, $P = 0.004$; removal: $Z = 3.15$, $P = 0.002$). However, there was no difference in the detection and removal of Jeffrey pine caches between the sites. At the Little Valley site, the detection rate of peony caches was significantly higher than that of Jeffrey pine caches ($Z = -2.66$, $P = 0.008$), with an estimated mean number of days before detection of 13.9 d for peony and 31.0 d for Jeffrey pine seed caches.

However, rodents did not always remove peony seeds after they dug them up, whereas they always removed
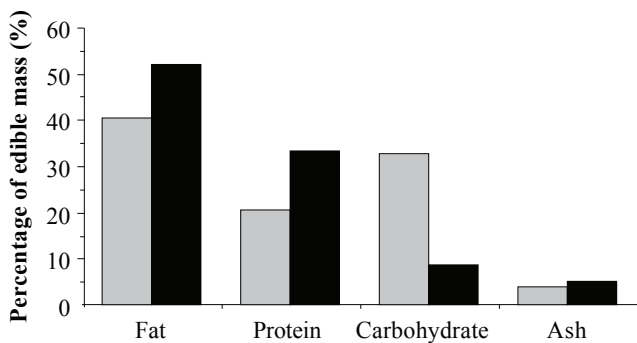


FIGURE 2. Seed nutritional analysis (percent of edible mass) for peony (grey) and Jeffrey pine (black) seeds. Nutritional analysis was performed by Ward Laboratories with a sample of 120 seeds of each species.

TABLE I. Number of rodents caught at 3 sites in 2009 and 2010 (200 trap days for each year and site). Species that are thought to occur at a site but that were not captured are denoted with a zero.

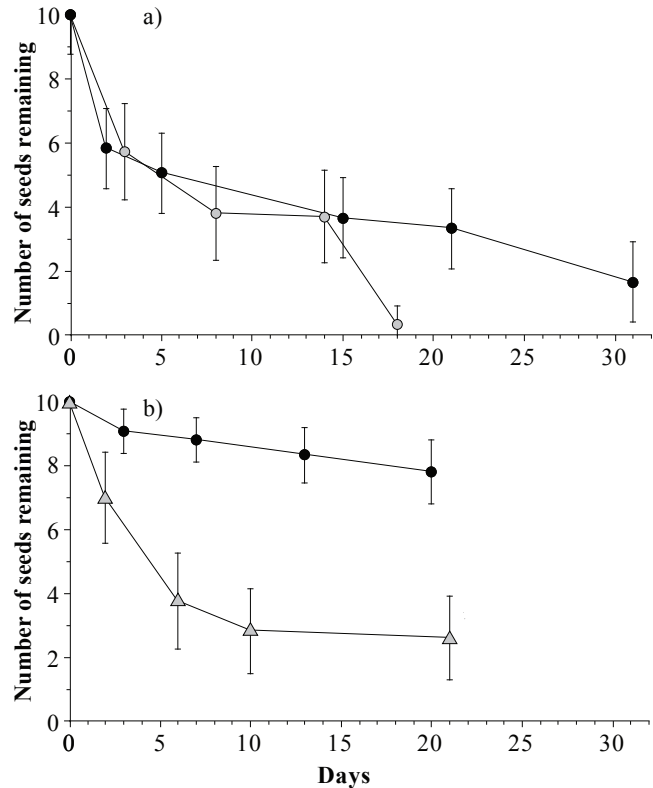| Species | Little Valley 2009 | Little Valley 2010 | Waterfall Fire 2009 | Red Rock 2010 |
|---|---|---|---|---|
| *Tamias amoenus* | 25 | 71 | - | - |
| *Tamias quadrimaculatus* | 2 | 1 | - | - |
| *Spermophilus lateralis* | 3 | 6 | - | - |
| *Peromyscus maniculatus* | 18 | 21 | 27 | 9 |
| *Dipodomys panamintinus* | - | - | 25 | 17 |
| *Dipodomys ordii* | - | - | 0 | 1 |
| *Perognathus parvus* | - | - | 7 | 43 |
| *Perognathus longimembris* | - | - | 0 | 1 |
| *Ammospermophilus leucurus* | - | - | 0 | 3 |



FIGURE 3. Harvest of peony seeds from beneath mature, seed-producing plants ($n = 10$ plants per year) in a) 2009 and b) 2010 (we placed 10 seeds in a tray under each plant). Black circles, Little Valley; grey circles, Waterfall Fire; grey triangles, Red Rock.

Jeffrey pine seeds when they detected a cache. So even though peony seeds were more quickly detected, there was no significant difference between the removal rates of the 2 seed species. Both the detection and the removal of mixed caches were significantly greater than those of Jeffrey pine caches (detection: $Z = -3.25$, $P = 0.001$; removal: $Z = -2.98$, $P = 0.003$) (Figure 5). The estimated mean number of days to detection and removal of mixed caches
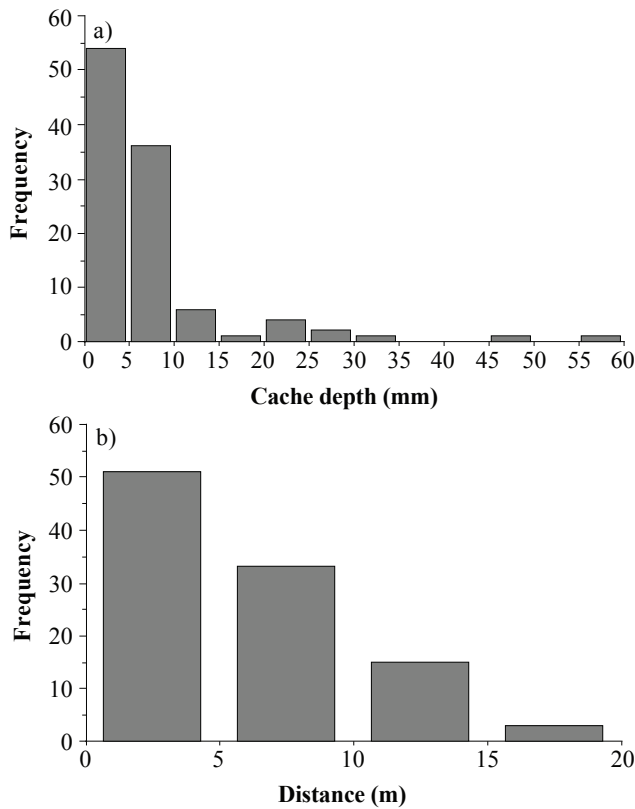


FIGURE 4. Histograms of seed cache characteristics from radio-labelled seeds placed under shrubs in Little Valley. Data from 2 y are pooled ($n = 102$ caches). a) Cache depth; and b) source-to-cache distance.

TABLE II. Number of caches made by rodents that harvested radioactively labelled peony seeds under plants in Little Valley in 2009 and 2010 and Red Rock in 2010. Each trial had 50 seeds on the surface under the focal peony plant. All data are means ± SE.

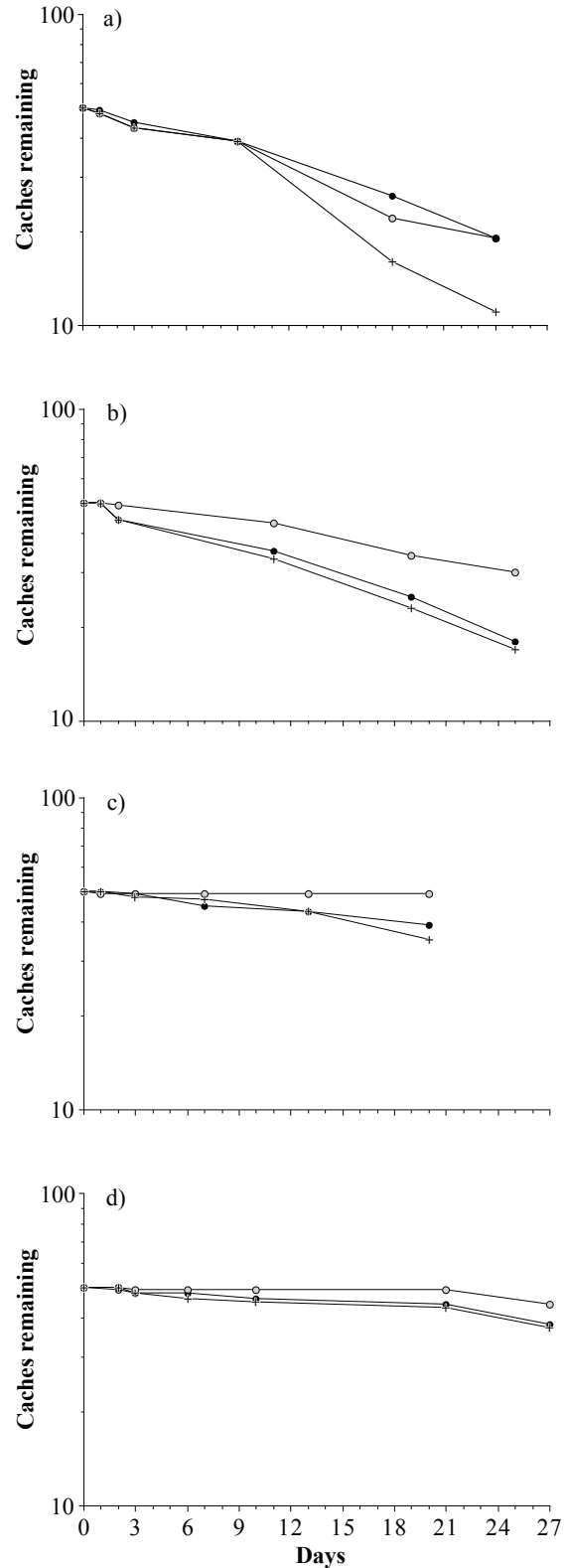| Location | Number of caches | Seeds per cache | Cache depth (mm) | Source-to-cache distance (m) |
|---|---|---|---|---|
| Little Valley | | | | |
| Junction 1 | 12 | 2.25 ± 0.6 | 14.17 ± 5.4 | 8.75 ± 1.5 |
| Junction 2 | 3 | 1.00 ± 0.0 | 2 ± 1.5 | 6.56 ± 0.8 |
| Meadow 1 | 5 | 1.00 ± 0.0 | 1.6 ± 0.24 | 1.85 ± 0.4 |
| Meadow 2 | 12 | 4.10 ± 3.1 | 11.0 ± 4.5 | 4.45 ± 0.6 |
| Meadow 3 | 5 | 1.00 ± 0.0 | 7.80 ± 1.4 | 1.00 ± 0.2 |
| Bitterbrush East 1 | 4 | 1.50 ± 0.3 | 3.25 ± 1.1 | 11.25 ± 2.3 |
| Bitterbrush East 2 | 31 | 1.10 ± 0.1 | 7.59 ± 1.5 | 8.04 ± 0.7 |
| Meadow 4 | 15 | 1.40 ± 0.1 | 3.97 ± 0.4 | 2.21 ± 0.3 |
| Rocky Ridge 1 | 12 | 2.55 ± 0.4 | 1.38 ± 0.3 | 7.79 ± 0.7 |
| Bitterbrush East 3 | 3 | 2.00 ± 0.0 | 4.83 ± 0.6 | 2.23 ± 0.1 |
| Red Rock | | | | |
| Red Rock 1 | 1 | 50 | 3.0 | 2.5 |



FIGURE 5. Removal and detection of artificial caches along transects. Two transects were established at each site in 2009 and 2010. This figure depicts the combined results from both transects at each site: a) Little Valley 2009, b) Little Valley 2010, c) Waterfall Fire 2009, and d) Red Rock 2010. Crosses, peony detection; grey circles, peony removal; black circles, Jeffrey pine detection and removal (pine seeds were always removed if detected).

were 11.7 d and 12.5 d, respectively, *versus* 31.0 d and 32.0 d, for Jeffrey pine caches.

There was no significant difference between the rates of detection and removal for any of the cache types at the Waterfall Fire site. The mean number of days before detection of the peony, mixed, and Jeffrey pine caches were 29.1 d, 29.2 d, and 35.4 d, respectively. The mean number of days before removal of peony and mixed caches was 41.2 d and 31.6 d, respectively.

There were no significant differences in cache detection between sites in 2010 ($Z = 1.06$, $P = 0.290$), so the data for both sites were combined for analysis. Again, the detection rate of peony caches was significantly higher than that of Jeffrey pine caches ($Z = -2.77$, $P = 0.006$). The detection rate of mixed caches, although lower than the detection rate of peony caches, was also significantly higher than the detection rate for Jeffrey pine caches ($Z = -2.456$, $P = 0.014$). There were no significant differences between the removal rates of the different cache types. The rates of detection and removal were extremely slow, and the estimated mean number of days before detection of the peony, mixed, and Jeffrey pine caches was 56.3 d, 61.5 d, and 124.5 d, respectively, with removal of mixed and peony caches taking somewhat more time.

SEED GERMINATION

In spring 2009, the average percent germination for seeds buried at 5 mm was 68.7 ± 18.1% for fresh peony, 30.0 ± 15.3% for dry peony, and 46.7 ± 14.7% for Jeffrey pine (Table III). Seed depth significantly affected the probability of seedling emergence, with more deeply buried seeds being more likely to produce seedlings ($P < 0.001$). In spring 2010, the 2 treatments with the highest average percent germination were Jeffrey pine seeds buried at 1 cm (55.6%) and fresh peony seeds at 1 cm (52.8%) (Table IV). The 2 treatments with the lowest average percent germination were fresh peony on the surface (2.8%) and dry peony on the surface (8.3%) (Table IV). Differences in germination of seed types were not significant; however, seed depth significantly affected the probability of seedling emergence, with more deeply buried seeds being more likely to produce seedlings ($X^2 = 72.6$, df = 2, $P < 0.001$). There were also significant differences in seedling emergence based on site ($X^2 = 23.6$, df = 1, $P < 0.001$) and plot within sites ($X^2 = 38.1$, df = 2, $P < 0.001$).

## Discussion

This study demonstrated that several species of rodents disperse *P. brownii* seeds. Seed removal from mesh trays under plants and video recordings from Little Valley confirm that chipmunks will take peony seeds from under plants. The clumping of seed caches at several sites indicates that chipmunks are probably responsible for making most of the caches we found. Yellow-pine chipmunks often fill their cheek pouches with seeds, travel a short distance, and then make 5–10 caches in a small area (Vander Wall, 1995b). The presence of some relatively large caches (3 or more seeds) and caches at relatively great distances (>10 m) from the focal plant also suggest that chipmunks were caching the peony seeds. The farthest peony caches found in Little Valley were 19.4 m from the focal plant in 2009 and 11.8 m from the focal plant in 2010. At several other sites (Table II), many shallow, 1-seed caches at short distances from the seed source suggest that deer mice were probably the disperser as this type of cache matches their behaviour (Vander Wall *et al.*, 2001; Hollander & Vander Wall, 2004). Unfortunately, the video cameras were unable to capture images at night, so there is no photographic evidence of their harvesting behaviour. We found 1 larder that contained 32 peony seeds and many small buckwheat seeds in a burrow in Little Valley in 2009 that appeared to have been made by a deer mouse. Golden-mantled ground squirrels were also videotaped taking peony seeds from under plants in Little Valley. However, these ground squirrels might not be very effective dispersers of seeds. They usually make caches that are too deep for seedling emergence and that contain so many seeds that emerging seedlings would experience intense competition for resources (Briggs, Vander Wall & Jenkins, 2009; Vander Wall, Enders & Waitman, 2009).

Seeds were taken by rodents from under focal plants during seed-tracking trials at the Red Rock site. However, there was little evidence that they scatter-hoarded seeds. Only 1 large cache, containing 50 seeds buried under a thin layer of plant litter, was located. The large number of seeds contained in this cache and the fact that it was under a shrub suggests that a Great Basin pocket mouse or a Panamint kangaroo rat may have been responsible (Hollander & Vander Wall, 2004).

Although rodent caching appears to be the primary means of dispersal of North American peonies, observations

TABLE III. Percentage emergence of seedlings in spring 2009 from germination plots in Little Valley that were established in autumn 2008. Plots contained 3 seed types (Jeffrey pine, dry peony, and fresh peony) that were buried at 5 mm depth.

| Site | Jeffrey pine (%) | Dry peony (%) | Fresh peony (%) |
|---|---|---|---|
| 1 | 58.0 | 43.3 | 52.0 |
| 2 | 52.0 | 33.3 | 88.0 |
| 3 | 30.0 | 13.3 | 66.0 |
| Average | 46.7 | 30.0 | 68.7 |

TABLE IV. Percentage emergence of seedlings in spring 2010 from germination plots at Little Valley and the Waterfall Fire site that were established in autumn 2009. Plots contained 3 seed types (Jeffrey pine, dry peony, and fresh peony) at 3 depths (surface, 5 mm, 10 mm).

| Site | Jeffrey pine (%) | | | Dry peony (%) | | | Fresh peony (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | Surface | 5 mm | 10 mm | Surface | 5 mm | 10 mm | Surface | 5 mm | 10 mm |
| Little Valley-1 | 0.0 | 44.4 | 55.6 | 11.1 | 22.2 | 22.2 | 0.0 | 0.0 | 33.3 |
| Little Valley-2 | 66.7 | 77.8 | 44.4 | 22.2 | 66.7 | 88.9 | 11.1 | 88.9 | 100.0 |
| Waterfall Fire-1 | 0.0 | 44.4 | 100.0 | 0.0 | 11.1 | 33.3 | 0.0 | 0.0 | 55.6 |
| Waterfall Fire-2 | 0.0 | 0.0 | 22.2 | 0.0 | 0.0 | 22.2 | 0.0 | 0.0 | 22.2 |
| Average | 16.7 | 41.7 | 55.6 | 8.3 | 25.0 | 41.7 | 2.8 | 22.2 | 52.8 |

at the Waterfall Fire site also indicated that some of the fallen peony seeds may have moved short distances by gravity, rain splash, or wind, which caused them to roll along the surface and, possibly, become shallowly buried. Establishment by these mechanisms appears to be infrequent.

Results of the germination trials indicated that burial increases the probability of seedling emergence for both peony and Jeffrey pine seeds. In the plots established in 2008, there was a decrease in the probability of seedling emergence for the peony seeds that had been air dried on the soil surface before burial (Table II). These seeds appeared shriveled after extended exposure on the ground surface. The thin hull may make the seeds vulnerable to desiccation over time. In the plots established in 2009, depth of burial was shown to be more important than seed type (*i.e.*, fresh *versus* dry; Table IV).

The slow removal of peony seeds from under source plants (Figure 3) and from discovered caches (Figure 5) indicates that peony seeds are a low preference food item compared to Jeffrey pine seeds. The seeds of Jeffrey pine, the reference species in this study, are known to be a highly preferred food item for rodents in Little Valley; quantities of 150 or more seeds offered to rodents in other studies in Little Valley were typically removed overnight (*e.g.*, Vander Wall, 1994a; 1995b; 2002). In comparison, removal of 50 peony seeds in this study often took a week or more. Nutritional analysis of these 2 seed species is consistent with this conclusion (Figure 2); rodents usually prefer seeds high in lipids (*e.g.*, Smith & Follmer, 1972). The more rapid rate of excavation of peony caches by rodents suggests that peony seeds can be detected more easily, probably because of a stronger odour, than Jeffrey pine seeds, but in many cases the rodents did not find the peony seeds desirable enough to remove them. In Little Valley in 2009, for example, the mean number of days to remove peony seeds (approximatively 31 d) was more than twice the number of days that it took to detect the cache (approximatively 14 d). In contrast, Jeffrey pine caches were always removed if detected. In addition, the higher rate of detection of peony caches in Little Valley in 2009 suggests that once mix caches were detected due to the presence of the peony seeds, the rodents would take the contents of the cache due to the presence of Jeffrey pine seeds. There was no significant difference in the detection or removal of peony and Jeffrey pine caches at the Waterfall Fire site in 2009. The higher rate of detection and removal of peony caches at Little Valley compared to the Waterfall Fire site was unexpected, because some desert rodents have a better sense of smell than rodents in more mesic habitats (Vander Wall *et al.*, 2003) and because heteromyid rodents have a preference for carbohydrate-rich seeds (Jenkins & Ascanio, 1993). However, this may have been due to the greater availability of alternative seed sources at the Waterfall Fire site. In addition, the somewhat wetter conditions found in Little Valley may have increased the rodents' ability to locate seed caches (Vander Wall, 1998).

*Paeonia brownii* appears to be adapted to this mode of seed dispersal. Attributes that facilitate dispersal of seeds by scatter-hoarding rodents include large, richly-coloured brown seeds contained in downward-facing pods that dehisce and drop seeds directly onto the ground. These traits are common to many species of nuts (Vander Wall, 2001). As far as we are aware, this mode of seed dispersal in Paeoniaceae has only evolved in North America, which may be because of arid conditions that select for water economy in plants (Beck & Vander Wall, 2010) and the presence of a guild of scatter-caching rodents (Price & Jenkins, 1986). Scatter-hoarding rodents bury seeds, which is known to be beneficial to plants in arid ecosystems (Price & Jenkins, 1986; Vander Wall, 1993; Beck & Vander Wall, 2010). Rodent preferences for these seed and fruit traits may select for the seed traits of North American peony species. Both *Ephedra* spp. (Hollander, Vander Wall & Baguley, 2010) and *Prunus* spp. (Beck & Vander Wall, 2010) exhibit a similar trend toward a scatter-caching dispersal syndrome in the North American species of these genera. Elsewhere, most members of Paeoniaceae have brightly-coloured seeds in conspicuous, upright, dehiscent pods that appear to be dispersed by frugivorous birds; this is thought to be the ancestral mode of dispersal in the group (Halda & Waddick, 2004). The mimetic seeds of some Old World peonies, such as *P. broteroi*, are known to attract naïve frugivorous birds, but experienced birds learn that the seeds do not provide them with a fleshy reward and seldom eat them (Galetti, 2002; Andrieu & Debussche, 2007).

As stated in the introduction, most rodent-dispersed plants are woody trees and shrubs, so it is important to explore how a relatively small herbaceous plant could evolve such a means of seed dispersal. Most plants dispersed by scatter-hoarding animals produce many large, nutritious seeds or nuts that are very attractive to foraging animals. However, plants have limited resources to allocate to reproduction; when seeds are large, the plant can afford to produce fewer of them (Smith & Fretwell, 1974). This helps to explain why plants that are dispersed through scatter hoarding are usually long-lived and large: this enables them to invest more energy in reproduction and to produce large quantities of propagules over their lifespan. To increase the number of seeds successfully dispersed, these plants tend to mast (Vander Wall, 2002; Jansen, Bongers & Hemerik, 2004), meaning that a population of a plant species will produce a large number of seeds in synchrony followed by a period of little seed production (Kelly, 1994). The need to produce large crops of large seeds or nuts presents a problem for small plants with limited resources, and this problem is exacerbated by the fact that plants that are dispersed by scatter-caching animals must offer most of their seeds as food "rewards" to animals for the transport and burial of the rest of their seeds (Vander Wall & Beck, 2011).

Relatively small plants like peonies could never adopt a strategy of producing many, large, nutritious nuts, because they lack the resources. The few attractive seeds that they could produce would be eaten quickly by animals. Thus, it appears that the peony's strategy rests on the fact that in most years it produces seeds that are edible but not highly desirable. The seeds are removed, albeit slowly, and often cached rather than eaten. These stores may serve as emergency rations, if needed. Rodents will also gather and cache more desirable seeds (*e.g.*, pine seeds), but those seeds will

also be preferentially retrieved and eaten. As time passes, rodents will be more likely to relocate and consume the more preferred seeds, like Jeffrey pine, from caches than those of wild peony. Thus, peony seeds may be slow to be cached, but they may also be slow to be relocated and eaten. Consequently, cached peony seeds will benefit from burial by rodents; many of them will be forgotten or left in the soil due to their low preference as food items. Because peony plants are long-lived, capable of storing a large amount of energy in their root system, and produce seeds every year, even low rates of seedling recruitment may be sufficient to maintain or to increase population sizes (Schlising, 1976).

As far as we are aware, there is only 1 other herbaceous geophyte that produces large seeds and is rodent-dispersed in North America, *Marah macrocarpus* (and probably its congeners). The physical characteristics of *M. macrocarpus* have been compared to *P. californica*, but the seeds of *M. macrocarpus* are high in both fat and protein content and contain no tannins (Borchert, 2004). *Marah macrocarpus* produces abundant flowers for 1–2 y after a fire and reverts to a non-reproductive state after the dominant cover plants begin to return to the disturbed area (Borchert, 2004). In addition, *M. macrocarpus* thrives in chaparral communities that experience a more frequent fire regime than that currently in place in high-elevation, dry forest and Great Basin Desert scrub communities. In contrast to peony plants, *M. macrocarpus* relies on rodents from neighbouring, unburned areas for its dispersal and burial (Borchert, 2004) and may require highly nutritious seeds to attract rodents into the fire-disturbed area. Like peonies, it has a large root that enables it to re-sprout quickly after a fire and exploit the opportunity to disperse while the abundance of other, neighbouring rodent-dispersed plants is reduced. Although peony plants seem to thrive for many years after a fire, unlike *M. macrocarpus* they consistently produce flowers and seeds during times when fire is absent and do not seem to rely on fire to stimulate reproduction. Thus, *M. macrocarpus* and *P. brownii* appear to have different dispersal strategies adapted to the ecosystems where they are found.

## Acknowledgements

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