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ECOLOGICAL BENEFITS OF MYRMECOCHORY FOR THE ENDANGERED CHAPARRAL SHRUB *FREMONTODENDRON DECUMBENS* (STERCULIACEAE)[1]

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Fremontodendron decumbens grows in a single county in central California, USA. Prior research showed that its elaiosome-bearing seeds are dispersed by the harvester ant *Messor andrei.* I tested several hypotheses regarding the positive role of ant-mediated dispersal to *F. decumbens*: (1) Does ant-mediated seed dispersal facilitate seed escape from rodent predation?; (2) Does ant processing of seeds stimulate germination?; (3) Are ant middens more suitable microsites for seed or seedling survival in unburned chaparral areas?; and (4) Do survival benefits of dispersal occur post-fire in the form of differences in seedling survival probabilities and, if so, why? Results of tests of each hypothesis were: (1) similar percentages of seeds placed on ant middens and under *F. decumbens* shrub canopies were destroyed by rodents, but seeds from which elaiosomes had been removed were more likely to escape rodent predation; (2) seeds processed by ants did not germinate more readily than seeds removed directly from shrub branches; (3) seedling predation was a major cause of mortality in unburned chaparral on both ant middens and under shrubs, and overall seedling survival did not differ between the two microsites; (4) post-burn seedling survival was significantly greater for seedlings dispersed away from *F. decumbens* shrub canopies, because dispersed seedlings were both less likely to be killed by predators and more likely to be growing in a gap created by the fire-caused death of an established shrub. I concluded that the major ecological benefit to *F. decumbens* of ant-mediated seed dispersal was elevated post-fire seedling survival resulting from enhanced escape by dispersed seedlings from both predation and competition.

Key words: ant-mediated seed dispersal; chaparral; fire ecology; *Messor andrei*; seed predation; seedling predation.

Seed dispersal is an important stage in the life history of plants. Benefits to plants of effective seed dispersal can include escape from herbivores and/or pathogens (Howe and Smallwood, 1982), minimizing competition from parent plants and/or siblings (Janzen, 1970; Higashi et al., 1989), colonization of openings (gaps) in existing vegetation (Thompson et al., 1998), initiation of new populations (Colas, Olivieri, and Riba, 1997; Cain, Damman, and Muir, 1998), and maintenance of genetic diversity by fostering gene flow between and within populations (Schnabel, Nason, and Hamrick, 1998).

Many cases of seed dispersal are mutualisms between plants and animals, in which animals disperse seeds or fruits and in exchange obtain a reward. Mutualistic seed dispersal commonly involves vertebrate animals (van der Pijl, 1982), such as mammals, birds, or even fish (e.g., Horn, 1997). Rarer is seed dispersal mediated by invertebrates, a taxonomic group that plays a major role in many animal-mediated cases of pollination but is not often involved with seed dispersal (Howe and Westley, 1988).

Among invertebrates, ants are the major taxonomic group that disperses seeds of plant species (Stiles, 1992), although members of other invertebrate groups may occasionally disperse seeds (e.g., Gervais, Traveset, and Willson, 1998). Most cases of ant-mediated seed dispersal involve collection of seeds (or fruits) that have elaiosomes attached to them. The elaiosome, which is often lipid-rich (Bresinsky, 1963), acts as a nutritional reward for the ants (Beattie, 1985; Morales and Heithaus, 1998; Wolff and Debussche, 1999). Ants collect the elaiosome-bearing diaspores and take them to their nests, where the elaiosome is consumed and the diaspore is then left in a chamber underground (Culver and Beattie, 1980) or ejected from the nest as waste (Handel, 1976; Horvitz and Beattie, 1980; O'Dowd and Hay, 1980; Buckley, 1982; Bullock, 1989; Harrington and Driver, 1995).

Ant-mediated seed dispersal is fairly common in some regions of the world, including eastern North America (Beattie, Culver, and Pudlo, 1979; Beattie and Culver, 1981; Handel, Fisch, and Schatz, 1981) and in Mediterranean-climate regions such as parts of Australia (Berg, 1975) and southern Africa (Milewski and Bond, 1982). It seems to be a fairly rare phenomenon in North American chaparral. Ant-mediated seed dispersal has been documented for only two chaparral shrub species: *Dendromecon rigida* Benth. (Berg, 1966; Bullock, 1974, 1989) and *Fremontodendron decumbens* Lloyd (Boyd, 1996). Keeley (1987) found elaiosomes present on the diaspores of only one of 45 shrub species he surveyed (that one being *F. californica* Torr.): thus, ant-mediated seed dispersal may be a genuinely rare phenomenon among shrubs in the chaparral flora. Other studies have documented ants as seed predators in chaparral (e.g., Horton and Kraebel, 1955; Keeley, 1977; Zammit and Zedler, 1988), suggesting that granivorous ants are a major threat to seeds in this community type.

Ant-mediated seed dispersal is widely viewed as a mutualistic interaction (Uphof, 1942; Buckley, 1982; Beattie, 1985; Handel and Beattie, 1990). If so, then some benefit should accrue to the plant in return for its energy investment in the elaiosome. Movement of seeds by ants may increase the probability of seed or seedling survival in a number of ways. One is escape from competition with parent plants/siblings (Higashi et al., 1989), although seedling competition can be a significant problem for ant-dispersed seeds that are concentrated in ant nests (Culver and Beattie, 1980). Many studies have shown that seeds of ant-dispersed plants are food sources for granivorous animals, such as rodents or birds (Heithaus, 1981;

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Smith, Ronsheim, and Swartz, 1986; but see Smith, Forman, and Boyd, 1989) or other arthropods (Ohkawara, Higashi, and Ohara, 1996). Ant-dispersed seeds may be less likely to suffer vertebrate predation because they have been moved to a relatively low-risk site (Bullock, 1974; Smith, Forman, and Boyd, 1989) or because removal of the elaiosome makes seeds harder for predators to find (Heithaus, 1981; Bond and Breytenbach, 1985; Espadaler and Gomez, 1997; but see Hanzawa, Beattie, and Holmes [1985] regarding rodent-repellent elaiosomes).

Other benefits may accrue to seeds dispersed by ants. Processing of seeds by ants may stimulate germination (Culver and Beattie, 1980; Horvitz and Beattie, 1980; Lobstein and Rockwood, 1993; Lisci, Bianchini, and Pacini, 1996; Mayer and Svoma, 1998). Movement to ant nests may benefit seeds after germination (Hanzawa, Beattie, and Culver, 1988), in part because ant nests may represent nutrient-enriched microsites that enhance seedling establishment (Culver and Beattie, 1978; Davidson and Morton, 1981; Oostermeijer, 1989; Gorb, Gorb, and Sindarovskaya, 1997; Eldridge and Myers, 1998; but see Rice and Westoby, 1986; Bond and Stock, 1989). It has also been proposed that ants aid seed survival in fire-prone communities by removing seeds to underground chambers, where they are less likely to be killed during a fire (Bond and Slingsby, 1984; Slingsby and Bond, 1985; Hughes and Westoby, 1992). Finally, dispersal over even relatively short distances may be enough to benefit seeds if safe sites for seed germination or seedling establishment are scarce, as has been suggested for arid Australian habitats (Andersen, 1988).

Fremontodendron decumbens Lloyd is an endangered shrub species found in one small chaparral-dominated area of the western foothills of California's Sierra Nevada (U.S. Fish and Wildlife Service, 1996). As with many endangered plant species, knowledge of its ecological relationships will allow managers to more effectively facilitate species recovery. One study, designed to characterize reproductive attrition in the species (Boyd and Serafini, 1992), showed that rodents were important predators of *F. decumbens* seeds. Approximately 90% of seeds placed beneath shrubs during each of two years were destroyed by rodent predators, suggesting that post-dispersal seed predation is a major reproductive bottleneck for this endangered species. However, Boyd (1996) showed that seeds of *F. decumbens* are dispersed up to 12 m away from parent shrub canopies by the harvester ant *Messor andrei* (Mayr). Ant nests are located in open areas in the shrub canopy, and *F. decumbens* seeds are typically discarded on middens that surround the ant nest entrance. The seeds are attractive to ants because each bears an elaiosome. This elaiosome contains an elevated lipid content and represents an energy cost to *F. decumbens* that decreases the energy available for seed production by at least 8% (Boyd, 1996).

If ant-mediated seed dispersal of *F. decumbens* seeds is a mutualism, then seed dispersal by the ants should provide an ecological benefit great enough to justify the energy cost to the shrub of producing elaiosomes. I tested several hypotheses regarding the positive role of ant-mediated seed dispersal to determine which, if any, provides a benefit for *F. decumbens.* These hypotheses are: (1) Does ant-mediated seed dispersal facilitate seed escape from rodent predation?; (2) Does ant processing of seeds stimulate germination?; (3) Are ant middens more suitable microsites for seed or seedling survival in unburned chaparral areas?; and (4) Do survival benefits of dispersal occur post-fire in the form of differences in seedling survival probabilities and, if so, why? Besides explaining the selective advantage of myrmecochory to a chaparral shrub species, answers to these questions should also provide information valuable to conservation efforts regarding this endangered species.

METHODS

Study species and study sites—*Fremontodendron decumbens* is very limited in its geographic distribution, growing only within a few kilometres of the summit of Pine Hill in El Dorado County, California. The plant is restricted to gabbro soils of the Pine Hill Formation, which also support several other rare and endangered plant species (Hunter and Horenstein, 1991). Most *F. decumbens* plants are found within the Pine Hill Ecological Reserve, a 97-ha protected area that encompasses the majority of the hill (U.S. Fish and Wildlife Service, 1996). This small (typically $<$2 m tall) shrub species grows mainly on the relatively rocky ridgetops of Pine Hill, scattered among more common chaparral dominants such as *Arctostaphylos viscida* C. Parry, *Adenostoma fasciculatum* Hook. & Arn., and *Heteromeles arbutifolia* (Lindley) Roemer (Boyd and Serafini, 1992).

My study sites were located on the main east-west ridge of Pine Hill. Portions of all the ridges of Pine Hill were disturbed in 1969 by the cutting of firebreaks (Stebbins, 1979) and, unfortunately, these ridges also supported the largest populations of *F. decumbens* then known to exist. Those shrub species that were capable of resprouting after fire or cutting (all of the aforementioned except *Arctostaphylos,* and including *F. decumbens*) recovered to form a 13-yr old (in 1982) stand. Study sites 1 and 2 were located on the ridge east of Pine Hill's summit. Site 2 was ~150 m from the summit in a rocky area containing a few *Pinus ponderosa* Laws. and *P. sabiniana* Douglas. Most of the shrub cover was *Adenostoma fasciculatum* and *Arctostaphylos viscida.* Site 1 was ~200 m farther east and contained the largest *F. decumbens* stand known. Most of the shrub cover on this site was *A. fasciculatum.* The third site (''burn site'') was an area on the western ridge, beginning 50 m from the summit, that was dominated by *Adenostoma fasciculatum* and *Arctostaphylos viscida.* The burn site, ≈1 ha in area and containing 43 *F. decumbens* shrubs, was prescribed-burned on 27 October, 1983. At the time of the fire, the relative humidity was 36%, the wind 0–6 kph, and fuel moisture (measured with a 10-h fuel stick) was 7% (Boyd, 1987). Approximately 80% of the area burned, including most (38) of the flannel bushes.

Hypothesis 1: Does ant-mediated seed dispersal facilitate seed escape from rodent predation?—This hypothesis was tested by two experiments. One used feeding trays to determine whether predation was influenced by distance from *F. decumbens* shrubs. The other was a long-term comparison of predation on ant middens and under shrub canopies using rodent exclosures.

Feeding tray experiment—A feeding tray was a 5 cm diameter plastic petri dish glued to a 10 cm long nail. Trays were placed in the field by driving the nail into the ground until the tray was firmly anchored but before the petri dish contacted the ground. The ~2-cm gap between the bottom of the dish and the ground surface prevented ants from climbing into the tray since they could not climb the smooth bottom and sides of the dish. Pairs of trays, the members of each pair spaced ~10 cm apart, were placed in three locations: under a flannel bush canopy and in the open 0.5 and 1 m distant from the edge of a shrub canopy. These distances were chosen because the largest gaps in the shrub canopy were 1–1.5 m in radius. Thus, the 1-m distance represented a location near the middle of a gap, whereas the 0.5-m distance represented sites located between the shrub canopy edge and the central portion of a gap. A total of ten sets of trays, with pairs of trays placed at each of the three distances comprising one set, were used for this experiment.

Seeds used for this experiment were collected from *F. decumbens* shrubs growing in the Arboretum of the University of California at Davis. At the start of the experiment, I placed five elaiosome-bearing seeds in one tray of each pair and five seeds from which I had removed the elaiosomes in the other tray. After 3 d I counted the seeds remaining in each tray. Trays with missing seeds were replenished with like seeds (either bearing or lacking elaiosomes) and the experiment continued for two more days. During this period, trays were checked at dawn and at dusk on each day, and missing seeds were replaced each time. Then the experiment was modified by adding five detached elaiosomes to each tray containing non-elaiosome seeds, and continued for two nights and one day. I replaced missing seeds (and elaiosomes) at each morning and evening check. Overall, I checked trays for seed removal a total of seven times during this experiment.

Data from the feeding trays were analyzed for visitation frequency (indicating discovery by a seed predator) as well as for numbers of seeds removed when visited. Visited trays were defined as those which had at least one seed taken during an observation interval. The influence of distance on visitation was examined separately for elaiosome-bearing and non-elaiosome seed trays by contingency table analysis. Distance effects for seed removal rates of elaiosome-bearing seeds and elaiosome-less seeds were also tested separately by the Kruskal-Wallis test.

For the last three data intervals, both trays of a pair contained five seeds and five elaiosomes, but the trays differed in that elaiosomes were attached to seeds in one tray and detached from seeds in the other. Tray visitation probabilities were compared by contingency table analysis. Influence of elaiosome presence or absence on seed removal rates was examined by the Wilcoxon paired-sample test, taking advantage of the pairing of trays in each location. We also used the Wilcoxon paired-sample test to determine whether seeds or elaiosomes were preferentially removed from trays in which both were present but detached from one another.

Exclosure experiment—The second experiment testing the seed escape hypothesis reflected longer term seed predation intensity on ant middens and under shrubs. I approached this question by comparing seed recovery from plots to which I added marked *F. decumbens* seeds (collected from shrubs on Pine Hill) and then recovered surviving seeds 8 mo later. Rodent predation of seeds on some plots was prevented by covering the plots with wire exclosures. Pairs of plots (20 × 10 cm) in each location (ant midden or under a nearby *F. decumbens* canopy) were selected in early November 1983, and each plot was sown with ten seeds from which the elaiosomes had been removed. I removed the elaiosomes from these seeds so that ants would not be attracted to them and disperse them (Boyd, 1996). I had marked each seed with nail polish, allowed them to air-dry for 2 wk before sowing to dissipate the solvent, and I sowed seeds with a metal spoon to avoid addition of olfactory cues due to handling. I randomly selected one plot of each pair and covered it with an exclosure (25 × 20 × 10 cm; L × W × H) made from 5-mm mesh hardware cloth, anchoring the exclosure with small bamboo stakes. Corners of the second plot in each pair were marked with small bamboo stakes. I established 19 replicates at site 1 and seven at site 2. Eight months later (in July 1984), I collected the litter and upper 1–2 cm of soil from each plot. I searched these samples for surviving marked seeds by floating off the litter in a large tub of water and sifting the coarse material at the bottom of the tub through a 1.4-mm mesh screen. Comparison of this method with hand-sifting of dry soil/litter samples showed it to be more effective in the recovery of viable *F. decumbens* seeds (which sink in water).

Effects of exclosure treatment and plot location on seed survival were analyzed by two-way Analysis of Variance (ANOVA). Counts of viable seeds remaining per plot were log-transformed prior to analysis so that data would more closely conform to the assumptions underlying ANOVA (Zar, 1996). Statistical significance was accepted at alpha ≤ 0.05.

Hypothesis 2: Does ant handling of seeds stimulate germination?—For this experiment, I used seeds from three sources: (1) seeds taken directly from mature capsules on shrub branches; (2) seeds marked with nail polish that had been given to ants and subsequently recovered after they had been ejected onto ant middens; and (3) naturally dispersed (unmarked) seeds found on ant middens. Seeds taken from mature capsules were collected from shrubs at site 1 during the summer of 1983 and stored at room temperature until this experiment was conducted. Seeds recovered from ant middens had been gathered from experiments conducted on site 1 during the summer and fall of 1983. Marked seeds were provided to foraging *M. andrei* and then collected from middens over the next few days as ants ejected them from their nests. Naturally dispersed seeds were collected from middens during searches for marked seeds. These experiments are described in more detail by Boyd (1996).

Half of the seeds from each source were heated in a forced-convection oven at 100°C for 5 min to stimulate germination (Boyd and Serafini, 1992), and half were not treated. I tested seed germinability by planting 75 seeds (5 seeds/pot in 8 cm square pots) from each source and heat treatment combination 1–2 cm deep in Thrift Mix (a combination of soil and potting mix). I placed the pots in a Percival Model PGW 108 growth chamber under a 17°C day/11°C night temperature regime and 16/8 h thermoperiod, and watered them as needed to keep seeds moist. I monitored seedling emergence every several days until emergence declined to <1 seedling/wk (this point occurred 4 mo after planting).

Effects of seed source and heat treatment on seedling production per pot were analyzed by two-way Analysis of Variance (ANOVA), with Fisher's Protected Least Significant Difference (PLSD) test used for post hoc mean separations. Counts of seedlings produced per pot were log transformed prior to analysis so that data would more closely conform to the assumptions underlying ANOVA (Zar, 1996). Statistical significance was accepted at alpha ≤ 0.05.

Hypothesis 3: Are ant middens more suitable microsites for seed or seedling survival in unburned chaparral?—*Seeds*—I collected dehiscing seed capsules from *F. decumbens* shrubs on other areas of Pine Hill during the summer of 1983, removed the seeds, and stored them at room temperature until fall. I stapled seeds into 1.4-mm mesh fiberglass screen sleeves (30 seeds/sleeve) and placed sleeves in pairs: one member of each pair under the canopy of an *F. decumbens* shrub and the other in an open area at least 50 cm beyond the canopy of any shrub. At each location I removed any litter, placed the sleeve on the soil surface, covered it with a piece of 7-mm mesh hardware cloth to prevent disturbance by rodents, and replaced the litter. Eight pairs of sleeves were placed in the field during late September 1983 and recovered in mid-June 1989, 5.75 yr later. Intact seeds in each sleeve were counted, and a 50-seed subsample, arbitrarily selected from those recovered from each location, was cut open to check endosperm condition. Seeds containing white, firm endosperm were considered viable, as has been shown by tetrazolium testing (Boyd and Serafini, 1992). Numbers of apparently viable seeds found in the pairs of sleeves were compared between shrub and open locations using the Wilcoxon paired-sample test.

Seedlings—I contrasted the suitability of ant middens and areas under *F. decumbens* canopies for seedling germination and survival by planting germinable seeds in both locations. I selected 16 middens and 16 nearby shrubs at site 1 and chose a pair of 20 × 10 cm plots at each location. I planted five seeds, made germinable by heat treatment (100°C, 5 min), in each plot and randomly selected one plot to be covered with a rodent exclosure (25 × 20 × 10 cm; L × W × H) made from 5-mm mesh hardware cloth. The exclosure was anchored with small bamboo stakes, and the corners of the adjacent unexclosed plot were also marked with small bamboo stakes. Seeds were planted ~2 cm deep in late November 1983, and I examined plots at ~2-wk intervals to count seedlings and record their condition until the last seedling died in July 1984.

Total seed germination per plot and mean seedling longevity per plot were analyzed by two-way ANOVA, using location and exclosure treatment as main effects factors and including the interaction term in the ANOVA model. Seedling longevity was defined as the time in days between the first record of a seedling and the midpoint between the last observation date it was observed alive and the following observation date. Germination data were log-transformed to better meet the assumptions underlying ANOVA, whereas longevity data (which were means per plot) were not transformed (Zar, 1996). Statistical significance was accepted at alpha ≤ 0.05.

Hypothesis 4: Do survival benefits of dispersal occur post-fire in the form of differences in seedling survival probabilities and, if so, why?—At 2–3 wk intervals, I surveyed the burned area for seedlings, marking each seedling with a colored stake and mapping its location. I revisited each seedling at 2–3 wk intervals until 13 mo after the fire, noting its condition during each visit. After germination ceased, I measured the distance from each seedling to the: (1) base of the nearest resprouting shrub, (2) base of the nearest shrub killed by the fire, and (3) edge of the nearest pre-fire flannel bush canopy. Because the intensity of the fire was low, burned branches were relatively intact and thus the general extent of the pre-fire shrub canopy could be reliably assessed. I considered seedlings growing beyond the edge of the pre-fire canopy of a *F. decumbens* shrub to be ''dispersed,'' whereas those found under a pre-fire *F. decumbens* canopy were labeled ''canopy'' seedlings.

Dispersed and canopy seedlings were further classified into several categories. First, I classified each seedling as being alive or dead by 25 November 1984, 13 mo after the fire. Second, seedlings that died by being bitten off below the cotyledons while young (during their first few weeks of age) were considered to have been destroyed by rodent predators. Finally, the distances from each seedling to the nearest dead shrub and the nearest resprouting shrub were compared. If the dead shrub distance was less than or equal to the resprouting shrub distance, that seedling was considered to be close to a ''gap'' in the chaparral community.

RESULTS

Hypothesis 1: Does ant-mediated seed dispersal facilitate seed escape from rodent predation?—*Feeding tray experiment*—Distance from the edge of a *F. decumbens* shrub canopy did not influence tray visitation. For trays containing elaiosome-bearing seeds, contingency table analysis of data from all seven data intervals showed no significant influence of distance on visitation (chi-square = 1.6, df = 2, $P = 0.46$). A similar result was found for trays containing non-elaiosome seeds. I analyzed data for only the first four data intervals for these trays, because during the last three data intervals I added elaiosomes into the trays along with the seeds and thus changed the experimental protocol. For the non-elaiosome seed trays, contingency table analysis again showed no significant influence of distance on tray visitation (chi-square = 2.6, df = 2, $P = 0.28$). Percentages of trays visited at 0, 50, and 100 cm away from the nearest canopy edge were 56, 64, and 69% for elaiosome-bearing seeds and 48, 33, and 33% for non-elaiosome seeds. All seeds were removed from most trays that were visited. In addition, some seeds were apparently consumed at the trays, as pieces of seed coat were left behind in the trays.

The number of seeds removed from visited trays also was not significantly affected by distance from a canopy edge. For trays containing elaiosome-bearing seeds, the Kruskal-Wallis test showed no significant influence of distance on the number of seeds removed (H corrected for ties = 4.4, df = 2, $P = 0.28$). Non-elaiosome seed trays had a similar result, with no significant influence of distance on the extent of seed removal (Kruskal-Wallis test, H corrected for ties = 0.25, df = 2, $P = 0.88$) seeds. Overall, at distances of 0, 50 and 100 cm, mean seed removal (±SD) per data interval per tray for those containing elaiosome-bearing seeds was 4.8 ± 0.57 ($N = 44$), 4.3 ± 1.2 ($N = 39$), and 4.2 ± 1.3 ($N = 46$). For trays holding non-elaiosome seeds, mean seed removal was 4.6 ± 1.1 ($N = 37$), 4.6 ± 1.1 ($N = 29$), and 4.6 ± 1.1 ($N = 27$) for trays at 0, 50, and 100 cm distant, respectively.

For the first four data intervals, pairs of trays differed in that one tray contained seeds without elaiosomes, whereas the other tray contained seeds attached to elaiosomes. Analysis of seed removal rates from these pairs of trays showed that significantly more seeds with elaiosomes attached were removed from trays by predators. After I excluded pairs of trays for which no seeds were removed from both trays, mean seed removal per data interval for trays containing elaiosome-bearing seeds was 4.3 ± 1.2 (SD, $N = 76$), whereas for trays containing seeds lacking elaiosomes the mean removal rate was only 2.7 ± 2.4 (SD, $N = 76$). The Wilcoxon paired-sample test showed that these removal rates differed significantly (tied Z value $= -5.2$, $P < 0.0001$).

Greater removal of elaiosome-bearing seeds could be due to two factors: greater visitation rates to trays containing seeds with elaiosomes attached, or greater removal rates of elaiosome-bearing seeds from trays containing seeds with attached elaiosomes. The visitation rate to trays with elaiosome-bearing seeds was significantly greater than for trays containing non-elaiosome seeds (63% vs. 38%, $N = 120$, contingency table analysis, chi-square = 15, df = 2, $P = 0.0001$). Seed removal was also greater for elaiosome-bearing seeds for those pairs of trays in which both trays were visited during a data interval. The mean number of seeds removed per data interval for trays containing elaiosome-bearing seeds was 4.2 ± 1.4 (SD, $N = 11$), in contrast to 2.3 ± 1.7 (SD, $N = 11$) for trays holding non-elaiosome seeds. The Wilcoxon paired-sample test revealed that these rates were significantly different (tied Z value $= -2.0$, $P = 0.041$). Thus, the greater removal of elaiosome-bearing seeds was due to a difference in both factors: greater tray visitation frequency and greater seed removal during a visit.

Confirmation of the importance of elaiosomes in enabling rodents to locate both the trays and the seeds within individual trays was provided by the portion of the experiment in which detached elaiosomes were placed into trays containing non-elaiosome seeds. Tray visitation was similar for trays with attached elaiosomes and for trays with detached elaiosomes: 60% for attached elaiosome trays and 52% for detached elaiosome trays (contingency table analysis, chi-square = 1.1, df = 1, $P = 0.29$). Seed removal from pairs of trays in which both trays were visited was greater for trays containing attached elaiosomes. A mean of 3.7 ± 1.3 (SD, $N = 16$) seeds were removed per visit for trays with elaiosome-bearing seeds, compared to 2.2 ± 2.3 (SD, $N = 16$) seeds per visit for trays in which elaiosomes were detached. This difference was significantly different (Wilcoxon paired-sample test, tied Z value $= -2.6$, $P = 0.0086$). For visited trays containing seeds with detached elaiosomes, predators preferred seeds over elaiosomes: mean seed removal per tray was 3.7 ± 2.1 (SD, $N = 47$) per data interval, whereas for elaiosomes it was only 1.9 ± 1.9 (SD, $N = 47$) per data interval. The Wilcoxon paired-sample test showed these removal rates were significantly different (tied Z value $= -3.0$, $P = 0.0027$). Even in trays containing seeds with elaiosomes attached, 23% of visited trays had at least one elaiosome left in them after the tray was visited. These elaiosomes had presumably been detached from their seeds during handling by predators and then were left behind when the seed was taken or consumed.

Exclosure experiment—Exclosures significantly decreased seed predation, but the magnitude of the effect was similar for both ant middens and locations under *F. decumbens* canopies. The ANOVA of the numbers of viable seeds recovered after 8 mo showed that the exclosure treatment was significant ($F_{1,100} = 16$, $P < 0.0001$), but neither the location term ($F_{1,100} = 2.2$, $P = 0.27$) nor the interaction term ($F_{1,100} = 0.41$, $P = 0.52$) was significant. The mean number of seeds recovered from exclosures on ant middens was similar to that recovered

TABLE 1. Germination of heat-scarified and non-scarified seeds either handled by ants or taken directly from dehisced capsules. Data are mean numbers of seedlings emerged per pot (± SD, *N* in parentheses).

Seed source	Seed treatment	
	100°C for 5 min	None
Mature capsules on shrubs	2.7 ± 1.3 (15)	0.13 ± 0.091 (15)
Marked seeds given to ants and recovered from middens	3.3 ± 1.2 (15)	0.27 ± 0.46 (15)
Unmarked seeds found in searches of middens	2.6 ± 1.1 (14)	0 (15)

from plots under canopies: 7.6 ± 3.1 (SD, $N = 26$) vs. 8.4 ± 1.9 (SD, $N = 26$). Open plots also had similar means in both locations: 0.92 ± 2.5 for ant midden and 0.89 ± 1.9 for canopy plots ($N = 26$ for both locations). The roughly 8.8-fold higher number of seeds recovered from under exclosures indicates relatively intense predation pressure in both types of microhabitats.

Hypothesis 2: Does handling of seeds by ants stimulate seed germination?—Ant-handled seeds were not more germinable than seeds taken directly from dehisced capsules. The ANOVA showed that heat treatment significantly boosted seed germination ($F_{1,83} = 320$, $P < 0.0001$). Untreated seeds germinated poorly (0–5.4%) in all cases, indicating that ants did not scarify the seeds during their activities (Table 1). This was verified by the lack of a significant interaction term in the ANOVA ($F_{2,83} = 0.40$, $P = 0.67$). The ANOVA also showed a significant effect of seed source on seed germination ($F_{2,83} = 3.2$, $P = 0.048$). Multiple comparison testing showed that marked seeds recovered from ant middens were more germinable than unmarked seeds found on ant middens (Fisher's PLSD, $P = 0.011$), but the marked seeds differed only marginally in germinability from seeds collected from *F. decumbens* branches (Fisher's PLSD, $P = 0.054$).

Hypothesis 3: Are ant middens more suitable microsites for seed or seedling survival in unburned chaparral?—*Seeds*—Seed survival after 5.75 yr was significantly greater for seeds placed under *F. decumbens* canopies than in open microsites. More intact seeds were recovered from sleeves placed under shrub canopies (25 ± 2.4, SD, $N = 8$) than in open locations (10 ± 6.0, SD, $N = 7$). This 2.5-fold difference was statistically significant (Wilcoxon paired-sample test, tied Z value $= -2.4$, $P = 0.018$). Most intact seeds were apparently viable, judging from visual inspection of endosperm condition. In a sample of 50 seeds from sleeves in each location, 92% of seeds from sleeves in open locations and 100% of seeds from sleeves under shrubs were viable. Combining the intact seed data with the viability data, 83% of seeds from under canopies and only 31% of seeds from open sites were viable after 5.75 yr.

Seedlings—Seed germination and emergence were not significantly affected by location or caging treatments. Total seedling number per plot showed no effect of the location ($F_{1,60} = 2.6$, $P = 0.11$), caging ($F_{1,60} = 0.56$, $P = 0.46$), or interaction terms ($F_{1,60} = 0.004$, $P = 0.95$). Mean seedling numbers per plot ranged from a low of 0.8 for open ant midden plots to 1.6 for exclosures under shrub canopies (Table 2).

TABLE 2. Comparison of ant middens and *F. decumbens* canopy locations as microsites for seedling production and seedling survival. Data for seedlings/plot and seedling longevity are means ± SD (*N* in parentheses). Predation percentages were calculated as the percentage of seedlings for which a fate was recorded (thus excluding those that were recorded as "missing").

Data	Plot type	Plot location	
		Ant midden	Shrub canopy
Seedlings per plot	exclosed	1.1 ± 1.1 (16)	1.6 ± 1.4 (16)
	open	0.81 ± 0.83 (16)	1.3 ± 1.0 (16)
Seedling longevity (d)	exclosed	23 ± 18 (10)	52 ± 24 (12)
	open	19 ± 23 (9)	32 ± 23 (12)
Predation (%)	exclosed	42	23
	open	75	44

Seedling survival was significantly greater under *F. decumbens* canopies. ANOVA revealed that location significantly affected survival ($F_{1,39} = 9.6$, $P = 0.0037$), whereas the exclosure treatment only approached significance ($F_{1,39} = 3.1$, $P = 0.087$) and the interaction term was not significant ($F_{1,39} = 1.4$, $P = 0.25$). Mean seedling longevity was greatest for canopy seedlings (either in exclosed or open plots), and also was greater in exclosed plots when compared to open plots in both locations (Table 2). No seedlings survived beyond July 1984. The cause of seedling mortality was unknown in some instances, but for others there were clear indications as to the cause of death. Many seedlings in the open plots were destroyed by rodents (which sliced seedlings off below the cotyledons and apparently consumed them, leaving a hypocotyl stump). Exclosed plot seedlings were also attacked, but by an insect which sliced seedlings off at ground level and left the detached seedling lying on the soil surface. As a result, predation was an important cause of mortality in both exclosed and open plots (Table 2). Overall, 32% ($N = 38$) of canopy and 55% ($N = 20$) of midden seedlings with known fates were destroyed by predation, but this difference only approached significance (contingency table analysis, chi-square = 3.0, df = 1, $P = 0.083$).

Hypothesis 4: Do survival benefits of dispersal occur post-fire in the form of differences in seedling survival probabilities and, if so, why?—A total of 1107 seedlings were discovered and marked during the rainy season (December–April 1984) immediately following the prescribed burn. Of these, 592 were located under pre-fire *F. decumbens* canopies and 515 were dispersed. Many seedlings died soon after germination, so that only 8.3% were alive by 25 November 1984, 13 mo post-fire and 10 mo after the first seedlings germinated. Survival of dispersed seedlings at 13 mo was 2.4-fold higher than canopy seedlings: 11.5 vs. 4.7%. This difference was statistically significant (contingency table analysis, chi-square = 17, df = 1, $P < 0.0001$).

Causes of mortality were numerous, but almost one-third (32.9%) of the 1015 seedlings that died by 13 mo post-fire were killed by rodents. Most of these rodent-killed seedlings were eaten while still in the cotyledon stage and were recognizable by the hypocotyl stump left behind. Significantly more of the canopy seedlings that died by 13 mo post-fire were killed by rodents (contingency table analysis, chi-square = 50, df = 1, $P = 0.0001$): 41% of canopy seedlings vs. only 21% of dispersed seedlings. Other seedlings died when they became deeply shaded under the canopies of resprouting shrubs. Seedlings growing closer to a dead shrub than to a resprouting shrub therefore were relatively close to a new opening in the shrub community. Significantly more dispersed seedlings were (by this measure) close to openings than canopy seedlings (contingency table analysis, chi-square = 48, df = 1, P = 0.0001). Only 2.9% of canopy seedlings were close to openings in contrast to 15% of dispersed seedlings, a 5.2-fold difference.

DISCUSSION

These results indicate that ant dispersal benefits *F. decumbens* seeds or seedlings in two ways. First, removal of the elaiosome makes seeds less likely to be taken by seed predators (presumably rodents). This suggests that the elaiosome provides olfactory cues that aid predators in finding seeds. My data support this hypothesis at two scales. Visitation to seed trays was greater for trays containing elaiosomes, indicating that elaiosomes aided rodents in finding trays. Similarly, seeds with attached elaiosomes were removed from visited trays at greater rates than seeds lacking elaiosomes. I interpret this to mean that rodents used elaiosomes as cues to find seeds in the trays as well as to locate the trays themselves. Finally, the elaiosome was apparently not the prime target of tray visitors: the seed was. This conclusion is supported by the greater removal rate for seeds in trays that contained separated seeds and elaiosomes. It is also consistent with the fact that, for trays that contained seeds with attached elaiosomes, one or more elaiosomes were sometimes left behind, whereas the seeds to which they had been attached were taken.

The attraction of seed predators to elaiosomes has been shown by other studies of elaiosome-bearing seeds (Culver and Beattie, 1978; Heithaus, 1981; Bond and Slingsby, 1984; Bond and Breytenbach, 1985), although in at least one case elaiosomes repelled rodent predators (Hanzawa, Beattie, and Holmes, 1985). For *F. decumbens,* removal of the elaiosome benefits seeds by aiding their escape from predators. However, this cannot be the selective advantage that counterbalances the energy cost of producing elaiosomes in the first place. Instead, rodents disrupt this mutualism by intercepting olfactory cues from the structure that attracts ants to *F. decumbens* seeds (Boyd, 1996).

The second benefit of ant-mediated seed dispersal for *F. decumbens* seeds only occurred after a fire had both modified the habitat and stimulated seeds to germinate. Seedlings resulting from dispersed seeds were significantly more likely to survive than those that germinated under the pre-fire canopy of a mature *F. decumbens* shrub. This survival advantage stemmed from two primary factors. First, rodent-mediated seedling predation was greater for canopy seedlings. This may have been a density-dependent effect, as seedling densities were notably greater under former shrub canopies. Density-dependent seedling predation is considered to be an important factor favoring seed dispersal from under a parent plant canopy (Howe and Westley, 1988). The second important survival advantage accruing to dispersed seeds was their increased probability of germinating in ''gaps'' in the shrub community. These gaps were created by the death of a pre-existing shrub during the fire, thus creating a safe site for seedling recruitment. Similar cases of enhanced recruitment following fire have been shown in other studies of endangered plant species (e.g., Lesica, 1999). Because *F. decumbens* is a post-fire resprouting species (Boyd, 1987), most of the burned mature shrubs in this study resprouted and thus eventually doomed seeds that germinated under their former canopies. This was reflected in the lower percentage of canopy seedlings that germinated near post-fire gaps (2.9%), as compared to dispersed seedlings (15%).

It is often assumed that seeds that are not dispersed away from a parent plant are essentially ''wasted.'' For example, Ohara and Higashi (1987) observed ground beetles consuming elaiosomes of *Trillium* seeds and concluded that the beetles were interfering with the efficiency of seed dispersal. In the case of *F. decumbens,* Boyd (1996) found that elaiosomes were attacked by small invertebrates soon after seeds were shed from capsules, and elaiosomes also began to rot when the rainy season began. Thus, elaiosomes were essentially destroyed after ~2 mo. However, this phenomenon may have two ecologically valuable results. First, destruction of the elaiosome will increase the probability of seed escape from predators. Second, seeds that remain under parent plant canopies are not necessarily ecologically useless for *F. decumbens.* In cases where the parent shrub is killed by fire (Boyd, 1987), seedlings germinating from these seeds will have a chance to recolonize that fire-created gap. Thus, the failure of seeds to be dispersed from the maternal plant functions to counter the possibility of fire-induced mortality among the original shrub population.

There are also costs associated with ant-mediated seed dispersal of *F. decumbens.* Rodgerson (1998) showed that predation by ants is an important threat to many elaiosome-bearing seeds. Boyd (1996) found evidence that some *F. decumbens* seeds taken by *M. andrei* were consumed by them and proposed that the increased thickness of the seed coat under the elaiosome helped to defend seeds as ants gnawed off elaiosomes. In this study, I found that seed longevity was decreased in open sites compared to under shrub canopies. This is likely due to more extreme temperature conditions on ant middens, which are located in openings in the shrub canopy (Boyd, 1996). Thus, a second cost of seeds being moved onto ant middens is decreased seed survival. I also found that ant middens are less suitable microsites for seedling establishment in unburned chaparral, again probably due to the more dry condition of those unshaded microsites. However, since most (almost 98%) of *F. decumbens* seeds remain dormant until after a fire occurs (Boyd and Serafini, 1992), differences in seedling survival in unburned chaparral are relatively unimportant ecologically.

There are other possible benefits to ant-mediated seed dispersal in *F. decumbens* that I was not able to experimentally investigate. Because *M. andrei* middens are constructed in relatively open areas in the chaparral (Boyd, 1996), fire intensity at such sites may be less than under shrub canopies. Also, ants may leave some seeds in underground galleries (Boyd, 1996) that could afford them some protection from fire. This has been shown to be a benefit for ant-dispersed seeds in other fire-prone vegetation types, such as occur in Australia (Hughes and Westoby, 1992) and South Africa (Bond and Slingsby, 1984; Slingsby and Bond, 1985). Unfortunately, my controlled burn was conducted on a relatively small area that contained few active ant nests at the time of the study. A more comprehensive burn experiment was precluded by the expense and risk of conducting a fire on a preserve surrounded by private residential property.

Finally, these results have relevance to the conservation of *F. decumbens,* one of many plants of global conservation concern (IUCN, 1997) for which ecological data are needed to formulate management plans (Boyd, 1994). First, the importance of *M. andrei* as a mutualist is confirmed. If ant-mediated seed dispersal were to cease, successful post-fire seedling establishment of *F. decumbens* would decline because *F. decumbens* seeds would not be dispersed to gaps opened by fires. Seedlings produced under mature shrubs would help ensure that those sites were occupied by *F. decumbens* even if a mature shrub died during a fire. However, eventually those mature shrubs would die and replacement by *F. decumbens* seedlings would fail, the latter situation aided by elevated seedling predation under burned shrub canopies. Thus, *F. decumbens* population size would ultimately decline without seed dispersal by *M. andrei.* It would likely take many fire cycles for this effect to seriously threaten a *F. decumbens* population, but it is clear that the long-term survival of *F. decumbens* requires protection of its dispersal mutualist. Bond and Slingsby (1984), studying ant dispersal of the shrub *Mimetes cucullatus* (L) R. Br. (Proteaceae) in South Africa, showed that replacement of native seed-dispersing ants by an introduced ant species can seriously disrupt ant-mediated seed dispersal of native plants. Monitoring the ant fauna of Pine Hill would help managers become aware of any threats to the native seed-dispersing ant species and, by extension, to the health of the endangered plant *F. decumbens.*

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