

## Dual role of harvesting ants as seed predators and dispersers of a non-myrmecorous Mediterranean perennial herb

Javier Retana, F. Xavier Picó and Anselm Rodrigo

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Ants have been traditionally considered either as predators or dispersers of seeds, but not both. That is, ant dispersal is restricted to myrmecochorous seeds, while almost all seeds removed by seed-harvesting ants are eaten. However, harvesting ants might be simultaneously antagonistic and mutualistic towards seeds. This study analyzes the predation–dispersal relationship between seed-harvesting ants and seeds of *Lobularia maritima*, a non-myrmecorous perennial herb, in order to disentangle the dual role of ants as dispersers and predators of *L. maritima* seeds. The results obtained confirm the role of harvesting ants as both predators and dispersers of the non-myrmecorous seeds of *L. maritima*. The removal activity of *Messor bouvieri* on *L. maritima* seeds is very important, particularly in autumn, which is the flowering and fruiting peak of this plant. It can be estimated that harvesting ants collect more than 85% of seeds, and almost 70% of them are effectively lost to predation. However, these granivorous ants also have drawbacks as seed dispersers. There is a relatively small percent of seeds collected by ants that escape predation, either because they are dropped on the way to the nest (16.4% of seeds harvested), or because they are mistakenly rejected on the refuse pile (0.9%). Abiotic dispersal of *L. maritima* seeds in the absence of ants occurs over very short distances from the plant stem. As seeds dispersed by ants reach a considerably greater distance than that obtained by gravity, this might represent a real advantage for the species, because it reduces intraspecific adult competition for seedlings, which directly influences seedling survivorship. These results challenge the generalization that seed removal by ants generally leads to successful seed dispersal if done by legitimate seed dispersers, or seed loss if done by seed consumers that eat them, and confirm that harvesting ants might have a dual role as both predators and dispersers of nonmyrmecorous seeds.

*J. Retana and A. Rodrigo, Unit of Ecology and Center for Ecological Research and Forestry Applications (CREAF), Autonomous Univ. of Barcelona, ES-08193 Bellaterra (Barcelona), Spain (javier.retana@uab.es). F. X. Picó, Dept of Ecology, Univ. of Nijmegen, Toernooiveld 1, NL-6525 ED Nijmegen, the Netherlands.*

The interactions between plants and ants are extraordinarily diverse (Beattie 1985, Huxley and Cutler 1991). From a quantitative point of view, in the Mediterranean basin the greatest impact that ants have on plants is in relation to seeds (Wolff and Debussche 1999). On the one hand, selective harvesting of particular seed species can affect the relative and absolute abundance of plant species (Brown and Human 1997). On the other hand,

foraging ants are likely to take seeds as food items to their nest, carrying them some distance away from the parent plant (Wolff and Debussche 1999). However, in both cases only completely positive or negative effects are considered. Thus, most studies focus on the impact of harvester ants considered strictly as seed predators or deal with myrmecochory as a benefit for a plant or group of plants (Wolff and Debussche 1999). In the first case, it

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is widely accepted that seed predation renders seeds non-viable for germination (Wang and Smith 2002). For this reason, harvester ants are generally viewed as seed predators (Díaz 1994, Retana and Cerdá 1994) and hence negatively affecting plant populations (Brown et al. 1979). Concerning seed dispersal, most studies (Levey and Byrne 1993) on ant-seed interactions have focused on seed dispersal of typical myrmecochorous plants whose elaiosome-bearing seeds are especially attractive to ants (Beattie 1985, Pizo and Oliveira 1998). Ants collect the elaiosome-bearing diaspores and take them to their nests, where the elaiosome is consumed and the intact seed is then deposited with other nest waste either in a nest midden or outside the nest (Smith et al. 1989, Kalisz et al. 1999, Boyd 2001). Myrmecochory is a widespread phenomenon, occurring in a great number of systematic groups of both plants and ants (Brew et al. 1989, Gorb and Gorb 1999).

These ideas may be summed up in two extremely simple considerations: (i) pre- and post-dispersal seed harvesting is almost equivalent to seed predation (Levey and Byrne 1993, Boyd 1996), because it is usually accepted that all seeds removed by seed-harvesting ants are taken into nests and consumed (Andersen 1988, Schupp 1990); and (ii) myrmecochory is synonymous with seed dispersal by ants, that is, ant dispersal is restricted to myrmecochorous seeds. Here we see one of the dangers of typological labels. The most common outcome of an ant-seed interaction typically determines whether the ant is classified as a seed predator or disperser. However, in many cases the rarest outcome may be more important to the plant than the typical outcome (Levey and Byrne 1993). This is especially important for the still largely unexplored interactions between ants and seeds from nonmyrmecochorous plants (Pizo and Oliveira 1998). In these cases, as seed predators are by definition detrimental to seeds, possible benefits of seed harvesting by granivore ants are often not considered (but see Levey and Byrne 1993, Pizo and Oliveira 1998, Detrain and Tasse 2000). There are contradictory opinions on the trade-off of benefits and costs of the effect of ants on seeds of nonmyrmecochorous plants. It is generally held that ant predation on seeds has a large impact on plant recruitment (Samson et al. 1992, Brown and Human 1997). However, ants might be simultaneously antagonistic and mutualistic towards these plants, killing most seeds but significantly benefiting some (Levey and Byrne 1993, Boyd 1996). These benefits for the plant may be rare and difficult to study, but we should not assume they are unimportant: in a system in which most seeds die, rare events such as seed placement on refuse piles or safe sites may be important determinants of recruitment (Dean and Yeaton 1992, Levey and Byrne 1993, Vorster et al. 1994). Compared with dispersal systems by other animals, seed dispersal by ants generates short distances

(Hughes et al. 1994, Gómez and Espadaler 1998, Greene and Calogeropoulos 2002). Nevertheless, even these short dispersal distances can represent substantial advantages, including reduction of parent-offspring competition and of density-dependant predation, as well as dispersal towards microsites favorable to germination (Levey and Byrne 1993, Ohkawara et al. 1996, Kalisz et al. 1999, Wang and Smith 2002).

This study analyzes the predation-dispersal relationship between seed-harvesting ants (*Messor bowieri* Bond.) and seeds of *Lobularia maritima* (L.) Desv., a non-myrmecochorous perennial herb that shows an exceptionally extended flowering and fruiting (Picó and Retana 2000). The two components of the system, ants and seeds, show a partial coincidence throughout the year, which determines the intensity of the relationship in each period. Thus, the activity of *M. bowieri* outside the nest extends from March to November, with a peak in early autumn (Cros et al. 1997), while the flowering and fruiting period of *L. maritima* extends from September to June, also with a maximum in early autumn (Bosch et al. 1997, Picó and Retana 2001). Our objective is to disentangle the dual role of ants as dispersers and predators of *L. maritima* seeds.

## Methods

### Study species

*Lobularia maritima* (L.) Desv. (Brassicaceae) is a native, herbaceous perennial that occurs in coastal zones, dunes and scrublands in the Mediterranean basin (Bolós et al. 1993). This herb is a short-lived plant with a lifespan of approximately three years. Plants form a basal rosette of ascending flowering stalks. Flowers are hermaphroditic and insect-pollinated (Bosch et al. 1997, Gómez 2000, Picó and Retana 2000), and present a high degree of self-compatibility (Picó and Retana, unpubl.). Fruits are siliqua containing two seeds (1–2 mm length) that do not have any dispersal mechanism, and fall by gravity after fruit dehiscence. Flowering and fruiting last for almost 10 months, from early September to late June (Bosch et al. 1997, Picó and Retana 2001), with a flowering and fruiting peak in autumn (Picó and Retana 2000).

*Messor bowieri* (Bond.) is a seed-harvesting ant with broad Mediterranean distribution, particularly in open and sunny habitats near the coast (Bernard 1968). Its dietary spectrum is chiefly composed of seeds and, to a lesser extent, other plant debris (Cerdá and Retana 1994). Daily foraging activity of *M. bowieri* is strictly diurnal, but changes from unimodal with one peak at midday in spring and autumn, to bimodal in summer (Cerdá and Retana 1994, Cros et al. 1997). Seasonal activity of *M. bowieri* colonies extends throughout the year, although from December to April only occasional

workers are found outside the nests (Cerdá and Retana 1994). The greatest outside activity occurs in autumn (Cros et al. 1997). Colonies form narrow trails of 1.5–10 m along which workers move before they diverge on their individual paths; these foraging columns are temporary, and rotate around the nest depending on seed availability, even from the morning to the afternoon of the same day (Cerdá and Retana 1994). *Messor bowieri* collects both *L. maritima* fruits and seeds directly on the plant, but also seeds fallen on the ground.

### Study site

The study site is located at Collserola Park, a protected area just beside Barcelona (NE Spain; 41°24'N, 2°6'E), 280 m above sea level on an eastern slope facing the Mediterranean coastline. The climate is typically Mediterranean, with 620 mm of mean annual rainfall, and mean monthly temperatures with a maximum of 23.2°C in August, and a minimum of 7.8°C in January. The site is a scrubland dominated by *Hyparrhenia hirta* L. and shrub species, such as *Cistus monspeliensis* L., *Spartium junceum* L. and *Ulex parviflorus* Pourr, and with some sparse *Pinus pinea* L. trees. *Lobularia maritima* is one of the most abundant herbaceous species in the plant community studied, greatly outnumbering other entomophilous species from October to March (Picó and Retana 2001). *Messor bowieri* is the most abundant seed harvesting ant species in the area, although *M. capitatus* is also present (Retana and Cerdá 2000).

### Seed removal by ants

To analyze the effect of the distance from the plant to the ant nest on the removal rate of ants on *L. maritima* seeds, seed removal at different distances from *M. bowieri* nests was examined from September to April (nests were also sampled in May, but insufficient *L. maritima* plants were found to carry out the analysis). At the end of each month, four *L. maritima* plants were randomly selected at each of four different distances (0.5, 2.5, 5 and 10 m) from each of four *M. bowieri* nests. On each plant, five flowering stems were sampled, counting the total number of mature fruits and the number of cut pedicels denoting fruit removal by ants. The percent of fruit removal per plant and period was estimated as the average percent of fruits collected by ants in the five flowering stems per individual during this period. The effect of month, distance to the nest and nest on the percent of fruit removal was analyzed using a three-way ANOVA. Inspection of residuals was carried out to check for normality and homoscedasticity. To normalize the data, values were arcsine-square root transformed.

### Importance of *L. maritima* seeds on *M. bowieri*'s diet

Observations of the efficiency of seed collection throughout the activity season of *M. bowieri* were carried out in 4–7 seven nests. Loaded and unloaded workers arriving at the nest were counted separately in order to calculate the proportion of workers carrying back a seed. To analyze the composition of the diet of *M. bowieri* throughout the year, in the same nests, one hundred items brought to the nest by foragers were collected for later identification in the laboratory from each nest and period. The proportion of *L. maritima* seeds and the number and diversity (H, Shannon index) of seeds were computed for the sample of seeds collected from each nest and period. One-way ANOVAs were carried out to analyze differences among months for the variables considered.

### Seed shadow in the absence of ants

The seed shadow (i.e. the area on the ground where the seeds fall from the plant; Wang and Smith 2002) in the absence of ants was examined for ten *L. maritima* plants planted in the experimental fields of the Autonomous University of Barcelona. At the beginning of the experiment, in early October, the base of each plant was flooded with a circular plastic seat of 1.5 m radius smeared with Tanglefoot® (The Tanglefoot Company, Michigan, USA) to catch the fallen seeds. One month later, the plastic seat was removed and carried back to the laboratory, where the distance of all seeds to the plant stem was measured.

### Seed dispersal by seed drops on ant foraging trails

The fraction of seeds collected by ants that were dispersed (that is, not consumed and abandoned far from the mother plant) and the dispersal distances were assessed in the field by quantifying seed drops by loaded *M. bowieri* workers returning to the nest over temporary trails. The study was carried out in autumn, the period of maximum activity of *M. bowieri* (Cros et al. 1997) and maximum abundance of *L. maritima* seeds (Picó and Retana 2000, 2001). In each of four nests, fifty workers carrying a *L. maritima* seed (or fruit) were pursued from the moment they collected the seed (either naturally found in the field or offered by the observer) until they reached the nest or dropped the seed. The distance the seed was moved (either to the ant nest or to the place where it was lost) and the total trail length were measured. The total duration of the period of observation was 120 h. The effect of the distance at which the seed has to be carried out (i.e. trail length) on the

probability of dropping the seed was analyzed using a logistic regression model.

### Seed dispersal by seed rejection to refuse piles

To evaluate the number of *L. maritima* seeds deposited in the refuse piles of *M. bowieri* nests (that is, again not consumed and potentially able to germinate), the entrance of five nests was cleaned up in autumn 2002. Twenty-five days later, the refuse piles produced in these nests were collected and transported to the laboratory. Then, the number of *L. maritima* seeds and fruits found among the debris were counted. The number of seeds rejected intact in the refuse pile was used as an estimator of the number of seeds non-eaten and, consequently, dispersed by ants. Seeds found in the refuse piles were placed in Petri dishes to monitor germination during 3 weeks in a dark germination chamber at 15°C. Seed germination values were compared to those obtained with seeds collected directly from the plants in order to estimate the change in germination ability due to ant manipulation. To determine the potential distances at which seeds could be dispersed if they were rejected on the refuse piles, we measured in the field the length of temporary trails of seven *M. bowieri* nests during alternative days along a month period.

To estimate the percent of seeds rejected to the refuse pile by *M. bowieri* nests, we computed the relationship between the number of seeds found in the refuse pile and the total number of *L. maritima* seeds transported to the nest during the 25-day period spent to produce the refuse piles analyzed in the laboratory. The total number of *L. maritima* seeds (NLS) transported to the nest during this period of time was computed as:

$$\text{NLS} = \text{NWR} \times \% \text{ EST} \times \% \text{ LSD} \times 25 \text{ days}$$

where NWR is the total number of workers returning to the nest per day and nest, % EST is the efficiency of seed transport (i.e. the proportion of loaded workers), and % LSD is the proportion of *L. maritima* seeds in the diet of the *M. bowieri* nest. These parameters are mean values from the observations obtained for each of the five nests sampled. In each nest, six-seven daily activity measures were carried out throughout the 25-day period by computing the number of loaded and unloaded workers returning to the nest during three minutes per hour throughout the whole daily activity period (from 11:00 a.m. to 3:00 p.m.). Values per hour were obtained by extrapolation, and daily values were obtained as the sum of all hourly values.

### Seedling survival in relation to the number of adult plants in the neighborhood

To estimate whether seedlings growing far from adult *L. maritima* plants had higher survival rates, we compared seedling survivorship in plots with different density of adult individuals. Existing data used in previous studies (Picó and Retana 2000, Picó et al. 2002) were reanalyzed to obtain such seedling survival. Data of the number of seedlings emerging during three flowering seasons (1995–1996, 1996–1997 and 1997–1998) of *L. maritima* were obtained in twelve 1 × 1 m<sup>2</sup> plots, where new seedlings were marked and monitored throughout the year. Seedling survival in each plot and year was estimated as the proportion of surviving seedlings at the beginning of the next flowering season related to the total number of seedlings emerging during the whole flowering season. As the seedlings of each flowering season were different cohorts and the number of adult plants also differed among years (depending on adult mortality), we considered the values of the same plot for the three flowering seasons considered as different replicates. The relationship between seedling survival and adult density was analyzed using linear regression analysis. The values of the number of adult plants per plot were log-transformed to normalize the data.

## Results

### Importance of *L. maritima* seeds on *M. bowieri*'s diet

Nearly half of the seeds collected by *M. bowieri* nests in October corresponded to *L. maritima* (Table 1), but the importance of the latter decreased in November, April and May, when other seeds, especially those of *Cistus monspelliensis* L. and *Hyparrhenia hirta* Pers., were preferred. *L. maritima* seeds are especially important in those periods of the year when the diversity of seed types in the diet (an indirect indication of the availability of different types of seeds in the field) is lowest (Table 1).

### Seed removal by ants

Seed removal on *L. maritima* plants depended on the distance to the closer *M. bowieri* nest and the month of the year (Table 2). Thus, removal of *L. maritima* seeds was higher in plants closer to (mean ± SE at 0.5 m: 15.0 ± 1.3% fruits collected; and at 2.5 m: 9.3 ± 1.0) than in those further away from a *M. bowieri* nest (at 5 m: 7.7 ± 0.6%; and at 10 m: 5.0 ± 0.4). There were also differences among months: November, October and, to a lesser extent, April showed higher removal values than the other months, when the outside activity of *M. bowieri* was very low or nil. The interaction between

Table 1. Composition of the diet of *M. bowieri* nests throughout the year. Mean ( $\pm$ SE) values of the percent of *L. maritima* seeds, and the richness and diversity (H, Shannon index) of seed types collected by foragers are shown for the different months of the activity period of ants. Those months that were not significantly different based on Fisher's protected LSD post-hoc test for the variables considered share a common letter.

Month	Number of nests	% <i>Lobularia</i> seeds	Richness of seed types	Diversity of seed types
April	4	10.0 $\pm$ 8.4 b	5.7 $\pm$ 0.7 bcd	0.64 $\pm$ 0.14 b
May	4	20.3 $\pm$ 20.3 ab	7.7 $\pm$ 1.0 abc	1.03 $\pm$ 0.20 ab
June	4	0 b	7.5 $\pm$ 0.3 abc	1.21 $\pm$ 0.08 ab
July	4	0 b	10.2 $\pm$ 0.9 a	1.47 $\pm$ 0.28 a
August	4	0 b	8.5 $\pm$ 1.3 ab	1.26 $\pm$ 0.28 ab
September	7	0 b	8.5 $\pm$ 1.3 ab	1.20 $\pm$ 0.20 ab
October	7	44.6 $\pm$ 16.1 a	5.5 $\pm$ 1.3 cd	0.69 $\pm$ 0.24 b
November	7	6.9 $\pm$ 3.9 b	3.6 $\pm$ 0.3 d	0.71 $\pm$ 0.12 b

Table 2. F-values from the ANOVA test of effects of month, distance to the nest, and nest on the percent of seed removal in *L. maritima* plants. Data have been arcsine square root-transformed.

Factor	DF	F	P
Month (M)	7	131.0	<0.0001
Distance to the nest (D)	3	77.1	<0.0001
Nest (N)	3	12.7	<0.0001
M $\times$ D	21	5.5	<0.0001
M $\times$ N	21	3.9	<0.0001
D $\times$ N	9	1.9	NS
M $\times$ D $\times$ N	63	0.3	NS
Residual	512		

the two factors was also significant: predation was always higher at the closest distance from ant nests, but differences among the other distances increased in the months with high seed removal compared to the months with low ant predation (Fig. 1). There were also significant differences in seed removal among the four

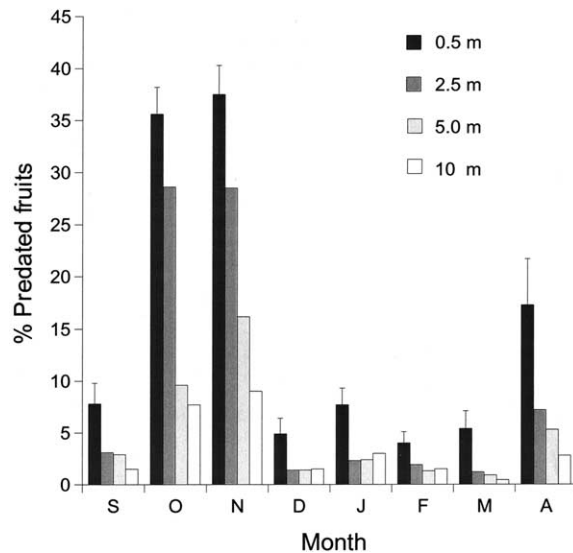


Fig. 1. Percent (mean $\pm$ SE) of *L. maritima* fruits collected by *M. bowieri* from September to April at different distances from the nest. The analysis was done on transformed data, but the figure presents untransformed data.

nests sampled, which also predated with different intensity in the different months (interaction month  $\times$  nest). The other interactions were not significant.

### Seed shadow in the absence of ants

Seed dispersal in the absence of ants occurred over very short distances from the plant stem (Fig. 2): most seeds (82%; mean value of 10 plants, with N = 2387 seeds collected) were found at less than 10 cm from the plant, while the mean distance was 4.9 cm (range: 0–72 cm).

### Seed dispersal by seed drops on ant foraging trails

During the transport of *L. maritima* seeds/fruits to the nest over temporary trails, 19 $\pm$ 4% of items (mean $\pm$ SE of four nests sampled) were lost before reaching the nest. Seeds were dropped slightly less than fruits (16.4% vs

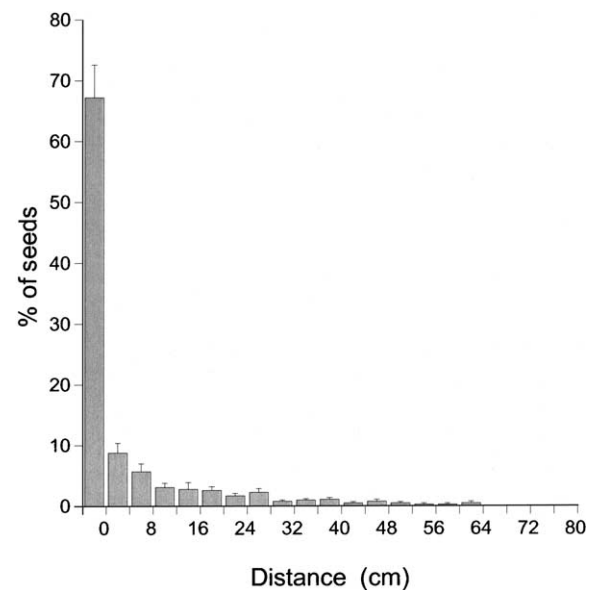


Fig. 2. Percent (mean $\pm$ SE of 10 plants sampled) of *L. maritima* seeds found at different distances from the plant stem.

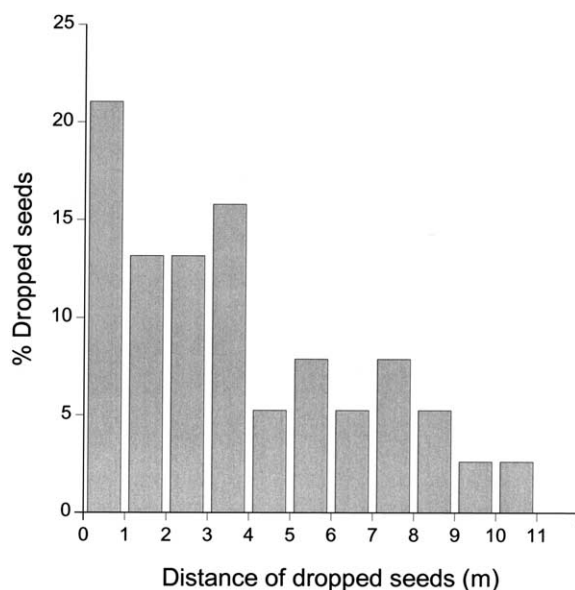


Fig. 3. Percent of *L. maritima* seeds or fruits dropped at different distances from the mother plant during the transport to the nest by *M. bowieri* foragers over temporary trails. N = 38 seeds or fruits dropped.

21.1%). Overall, mean dispersal distance was  $3.7 \pm 0.4$  m (N = 38), with a range of 0.3–10.1 m (Fig. 3). Foragers of the same nest collected almost none of the items dropped in the trail again, at least during the current daily activity period. Total trail length did not affect the probability of seed drop (logistic regression;  $\chi^2 = 1.8$ ,  $p = 0.18$ , N = 200).

### Seed dispersal by seed rejection to refuse piles

*Lobularia maritima* seeds or fruits were found in all the five refuse piles of *M. bowieri* nests analyzed. The number of *L. maritima* seeds rejected to these refuse piles was  $21 \pm 6$  seeds per refuse pile (N = 5 refuse piles sampled). The mean ( $\pm$ SE) number of *L. maritima* seeds transported to each *M. bowieri* nest during this period of time was  $2117 \pm 804$  seeds per nest (N = 5 nests). Thus, the percent of *L. maritima* seeds rejected to refuse piles was  $1.0 \pm 0.2\%$  of seeds collected. Ant manipulation and permanence in the refuse piles did not affect the germination of these seeds compared to control ones (percent of germination of control and refuse pile seeds in the laboratory: 34.7% and 41.3%, respectively;  $\chi^2 = 0.4$ ,  $p = 0.52$ , N = 100).

Ant trail distances, which determine the range of distances at which seeds could be dispersed when they were rejected on the refuse piles, had a mean ( $\pm$ SE) value of  $8.8 \pm 0.6$  m, with a range of 0.2–25.4 m (N = 82 trails).

### Seedling survival in relation to the number of adult plants in the neighborhood

Survival of seedlings depended on the number of adult *L. maritima* plants that they had in their neighborhood. As shown in Fig. 4, seedling survival at the beginning of the next flowering season decreased with the total number of adult plants (log-transformed) in the plot (linear regression;  $R^2 = 0.20$ ,  $F = 7.1$ ,  $p = 0.012$ , N = 36 plots). The regression had poor explanatory power most likely due to 100% seedling survival in some cases.

### Discussion

The results of this study confirm the role of seed harvesting ants as both predators and dispersers of the non-myrmecorous seeds of *L. maritima*. Granivorous ants are not usually very large in number, but they have a considerable impact on seeds (Brown et al. 1979, Díaz 1992, Auld and Denham 1999). In the study area, only four ant species eat seeds (Retana and Cerdá 2000), two have a diet essentially composed of seeds (*M. bowieri* and, in considerably lower numbers, *M. capitatus*), and two eat seeds occasionally (*Pheidole pallidula* and *Tetramorium semilaeve*). The removal activity of *M. bowieri* on *L. maritima* seeds is very important, particularly in autumn and, to a lesser extent, spring, when there are few seed types available and *L. maritima* seeds represent an important food resource for *M. bowieri* nests (Table 1). We found strong spatial and temporal evidences of this relationship: removal of *L. maritima* seeds decreased considerably far from a *M. bowieri* nest and in months when the outside activity of harvesting ants was very low or nil (Table 2). The

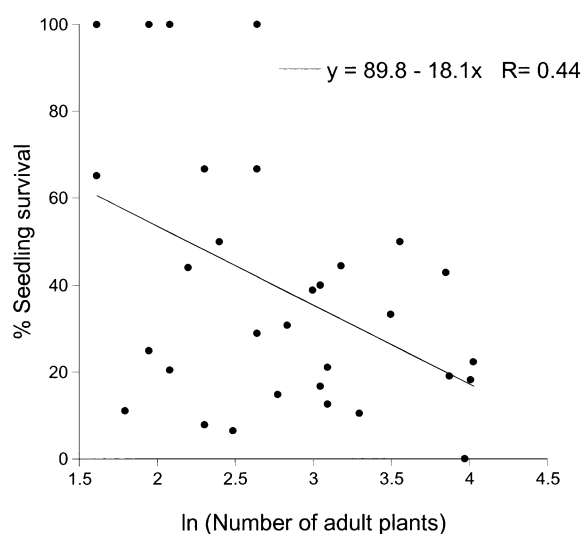


Fig. 4. Linear regression between the percentage of seedlings surviving in the next flowering season and the number of adult plants present in the plots (log-transformed). N = 36 plots.

important removal activity of this and other species of the genus *Messor* on many types of seeds has been widely described in the literature (Díaz 1992, Dean and Yeaton 1993, Brown and Human 1997). In the case of *L. maritima*, and considering joint pre- and post-dispersal removal (Picó and Retana 2000), it can be estimated that harvesting ants collect more than 85% of seeds, and almost 70% of them are effectively lost to predation (Fig. 5).

However, the most interesting aspect shown in the present study is that granivorous ants also have drawbacks as seed dispersers. Hughes and Westoby (1990) state that a high-quality ant disperser should have the following characteristics: first, all or some of the seeds collected should escape being eaten by the ant; second, the ant should behave in such a way that the seed is placed in a suitable site for germination and seedling establishment. The evidence of seed dispersal by ants has been widely described for myrmecochorous seeds (Ohkawara and Higashi 1994, Boyd 1996, 2001, Brown and Human 1997), which escape predation because they are transported to where the elaiosome is consumed, and they are then rejected from the nest as waste. There are fewer studies analyzing dispersal of

non-myrmecochorous seeds by seed-eating ants (Levey and Byrne 1993, Gorb et al. 1997, Detrain and Tasse 2000), a second type of ant dispersal called dyszoochory (Wolff and Debussche 1999). In this study, abiotic dispersal of *L. maritima* seeds in the absence of ants occurs over very short distances from the plant stem (Fig. 2), as has been described in other species without specific traits for seed dispersal (Quilichini and Debussche 2000). The majority of these seeds suffer either pre-dispersal or post-dispersal seed predation by harvesting ants (Picó and Retana 2000). For this reason, when there is a *M. bowieri* nest not very far from the plant, few seeds remain under the canopy of the parent plant (Fig. 5).

Nevertheless, not all seeds collected by ants are consumed; some of them escape predation, either because they are dropped on the way to the nest, or because they are mistakenly rejected on the refuse pile. Over trails, workers dropped up to 16.4% of harvested seeds (Fig. 5). It has been described a similar proportion of seed drops in other *Messor* species, such as *M. barbarus* (Detrain and Tasse 2000), but in these cases most seeds are recovered by nestmates within 24 h. We have not observed seed recovery by nestmates along *M. bowieri* trails, even when there is an artificially high accumulation of seeds. The main explanation for these differences refers to the foraging strategy of the two species: *M. barbarus* has a complex system of permanent trails (López et al. 1993), while the foraging columns of *M. bowieri* are temporary and are abandoned after a short period of time, which reduces the probability of workers recovering lost seeds. *Messor bowieri* workers perform an active process of load transfer between nestmates (such as that described in Ratnieks and Anderson 1999, Reyes and Haeger 1999) in almost 15% of cases (Anselm Rodrigo, unpubl.), but they do not collect seeds from the ground along the trail. Another means of dispersal of *L. maritima* seeds is by discarding them unharmed on refuse piles. This type of seed dispersal accounted for only 0.9% of *L. maritima* seeds harvested by *M. bowieri*. We are not able to assess whether this percentage is low or high because there are very few similar studies in the literature measuring the percent of rejection of intact seeds of non-myrmecochorous plants on refuse piles by seed-harvesting ants.

Anyway, the importance of this dispersal activity cannot be only measured by the number of seeds, but also by the distance at which they are dispersed further from the mother plant. Seeds on the trail are dispersed to a mean distance of 3.7 m from the mother plant, and those rejected to the midden to 8.8 m from it (Fig. 5); in other words, seeds dispersed by ants travel considerably further than by gravity. Although mean dispersal distances generated by ants are typically short (Hughes et al. 1994, Gómez and Espadaler 1998), such distances

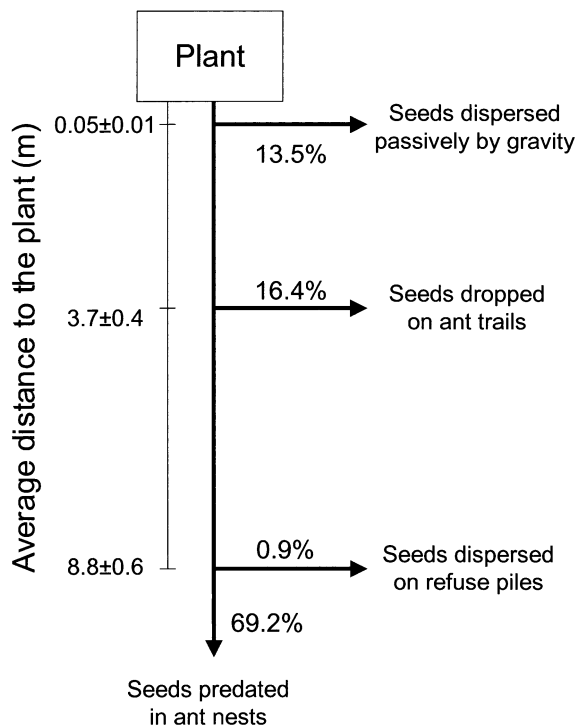


Fig. 5. Fate of the seeds produced by *L. maritima* plants in autumn. The mean distance from the mother plant at which the seeds are transported is indicated. The different ways total 100% of seeds produced. The information concerning the percentage of *L. maritima* seeds transported by ants has been obtained from Picó and Retana (2000), and the other percentages have been obtained relating the relative values shown in the text to the absolute proportion of seeds collected by ants.

may even strongly increase survival rates of seedlings, because they might suffice to reduce parent–offspring conflict (Westoby et al. 1982, Ohkawara et al. 1996, Gorb and Gorb 1999). The highest intensity of the relationship between *M. bowieri* ants and *L. maritima* seeds occurs in autumn, which is a particularly relevant period for the recruitment of this plant species. Thus, the maximum values of fruit production are reached in autumn and, although off-peak *L. maritima* fruits may escape more easily from seed predators than peak fruits, seedling establishment is also highest in this season (Picó and Retana 2000). In fact, the extended flowering season of *L. maritima* has very little effect on the population dynamics of this species, and seed production outside the autumn months is demographically meaningless (Picó et al. 2002). In this context, seed dispersal by ants in this period of the year represents a real advantage for the species, because it reduces intraspecific adult competition for seedlings, which directly influences seedling survivorship (Fig. 4).

The results shown in this study illustrate that interactions between plants and animals are complex and might be simultaneously antagonistic and mutualistic. Our results challenge the generalization that seed removal by ants generally leads to successful seed dispersal if performed by legitimate seed dispersers, or seed loss if performed by seed consumers that eat them. Many studies of post-dispersal seed fate assume that disappearance of non-myrmecochorous seeds is equivalent to seed predation (Schupp 1990), and ants are defined as “good” and “bad” seed dispersers, depending whether or not elaiosome is present. However, the dual role of ants, such as *M. bowieri* in the present study, as both predators and dispersers of seeds, confirms that the relationship between seeds and ants is not always evident. Not all *L. maritima* seeds removed by harvesting ants are taken into nests, and not all seeds taken into nests are consumed; that is, some of the seeds collected by ants might be dispersed. Although it is inherently difficult for researchers to determine the fates of seeds from parent plants (Wang and Smith 2002), it is important to analyze these mechanisms that indirectly reduce seed consumption, because they probably enhance the benefits to the plant and, moreover, could eventually suggest an evolutionary pathway to myrmecochory (Levey and Byrne 1993).

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