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Mucilage secretion by seeds doubles the chance to escape removal by ants

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Abstract Post-dispersal seed predation is a risk for plants in semiarid environments, leading to strategies to protect their propagules from seed collection by animals. In this study, we evaluated the importance of mucilage secretion in seeds as a mechanism to reduce seed collection by ants. We selected three Mediterranean species with strong mucilage secretion on their seeds which become sticky upon wetting. Seeds of *Rosmarinus officinalis*, *Fumana ericoides*, and *Fumana thymifolia* were exposed to ants and survival was compared between dry loose seeds and seeds glued to the soil with previously secreted mucilage. The study site was in the Sierra Calderona, 25 km north of Valencia (Spain). The ant–plant interaction was analyzed by scrutinizing seed collection by ants and by analyzing the waste piles of ant nests. To test survival, groups of 10 seeds were placed on the ground. Each group consisted of five control (dry) and five mucilaginous seeds (previously mucilage secreted) and was covered by the cover of a Petri dish modified to permit only the entry of ants. Seeds were inspected weekly for seed disappearance and the survival function (Kaplan–Meier estimator) was calculated. Seeds of the target species were important food items for ants and were actively collected, and more than 50 % of the experimental seeds that were glued to the ground with their own mucilage survived at the end of the study period but only 0–20 % of the control seeds survived after the same time of exposure. The implications for plant establishment of these findings are discussed.

Keywords Myxospermy · Seed dispersal · Seed predation · Seedling recruitment pattern · *Messor* · *Fumana* · *Rosmarinus*

Introduction

In semiarid environments, post-dispersal seed predation is a frequent risk and has the potential to influence plant populations and community dynamics (Louda 1989; Davidson 1993; Hulme 1996, 1998; Crawley 2000; Azcárate and Peco 2007). An effective strategy to escape massive seed collection can be of crucial importance for plant species in order to maintain their population densities above extinction thresholds.

Seeds can be consumed by mammals, birds, and insects (Janzen 1971; Crawley 2000; Kelt et al. 2004), but in some semiarid and arid ecosystems granivorous ants have the strongest impact on post-dispersal predation relative to other animal groups (Mares and Rosenzweig 1978; Morton 1985; Kerley 1991; Predavec 1997; Hulme 1998; Lopez de Casenave et al. 1998). Ants have a strong influence because of their ability to search on

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large areas for food and also the great number of seeds they can collect in a season (Hölldobler and Wilson 1990). For some plant species it has been reported that ants collect more than 85 % of available seeds, resulting in almost 70 % of seeds being effectively lost by predation (Retana et al. 2004).

Ants tend to collect a wide range of seeds depending on their availability (Hobbs 1985), but seed choice is also influenced by specific seed attributes, such as size, weight, and structure (Willott et al. 2000; Azcárate et al. 2005). Some seeds are, therefore, strongly collected and strategies to escape massive seed collection in these species could be especially effective.

Plants have developed mechanisms to escape from massive seed collection by animals, such as mechanical or chemical defenses, seed burial in the soil (Crawley 2000; Hulme and Benkman 2002; Schöning et al. 2004), or even seed dispersal by animals through rewarding with the fruit pulp or an elaiosome whereat the seed stays intact (Herrera 2002; Giladi 2006). Diaspores of many plants inhabiting semiarid habitats secrete a gel of polysaccharides around the seed or fruit coat which becomes sticky once they come in contact with water, getting them adhered to the soil upon drying (myxospermy) (Grubert 1974; Werker 1997). This hydrophilic, pectinaceous mucilage is deposited in the apoplast of epidermal cells in a compressed form during differentiation of the seed coat or pericarp, and is released on hydration to form a water-containing, gel-like capsule surrounding the seed (Western 2012). Once dried up, it glues the seed to the ground with a thin and strong layer and can rehydrate completely with the next rain or dew, drying and swelling for many times with almost no loss in volume. Rain and moistened soil are enough to release mucilage secretion, but Huang et al. (2004) and Huang et al. (2008) have shown that experimental and natural dew at nights is enough for seeds to secrete mucilage. This adherence to the ground has been suggested as a mechanism to reduce diaspore removal by erosion on slopes (García-Fayos et al. 2010) having the potential to act as a mechanism to escape from seed removal by ants. Seed harvesting by ants in the Negev Desert (Israel) was effectively slowed down and seed collection of *Salvia columbariae* in California (USA) was strongly reduced because of mucilage secretion (Fuller and Hay 1983; Gutterman and Shem-Tov 1997). Both the studies were done over very short time periods, between 2 days and a week, so the long-term efficacy of the mucilage was untested.

In this study, we tested the hypothesis that myxospermy effectively reduces seed removal by ants in the medium timeframe using a set of plant species inhabiting open, semiarid Mediterranean shrublands. Our objective was to test: (a) if seeds of the experimental plant species are of interest to ants; (b) if survival of seeds glued to the soil by mucilage is higher when exposed to harvesting ants than dry and loose seeds of these species; and (c) the implications of these findings for plant establishment in semiarid Mediterranean shrublands.

Methods

Study area

The study site is located in the municipality of Serra (39°39′N, 0°29′W) in Parque Natural de la Sierra Calderona, about 25 km north from Valencia (Spain) at 250 m altitude. The vegetation consists of open *Pinus halepensis* forest with a very rich layer of shrubs (*Rosmarinus officinalis*, *Erica multiflora*, *Cistus albidus*, *Rhamnus lycioides*, *Pistacia lentiscus*, *Thymus vulgaris*, *Helianthemum* spp., and *Fumana* spp.) and perennial grasses (*Stipa tenacissima* and *Brachypodium retusum*) reaching 50 % of soil cover in average (Andreu et al. 1998). Soils are loam and sandy-loam, rich in calcium carbonate (>40 %), poor in organic matter (<5 %), highly compacted, and nearly 3 % of bare soil is covered by crust (Andreu et al. 1998). Mean annual temperature is 17.4 °C and the mean annual rainfall is 467 mm (García-Fayos and Gasque 2006). The total study area spans about 1.5–2 ha and has very little human influence, with scarce agriculture in the surroundings and no exposure to grazing for decades.

Plant species

We use fruits of rosemary (*R. officinalis*, Lamiaceae) and seeds of needle sun roses (*Fumana ericoides* and *F. thymifolia*, Cistaceae) based on two criteria: their high amount of seed production or large seed size, both in combination with strong mucilage production. *R. officinalis* is a 0.5–1.5 m tall shrub widely distributed in the Mediterranean basin which produces large quantities of fruits. Fruits are soft nutlets (0.46 ± 0.024 mg, Lloret et al. 1999) that are an important food source for granivorous ants. For simplicity, we hereafter refer to them as seeds. *F. ericoides* and *F. thymifolia* are small-sized shrubs, up to 0.4 m tall (Güemes and Molero 1993). Seeds are relatively large (2.44 ± 0.054 and 1.08 ± 0.023 mg, respectively, Lloret et al. 1999) but they are produced in lower quantities than in *R. officinalis*. Despite their hard coats, seeds of *Fumana* are also strongly collected by granivorous ants (Arnan et al. 2010, author's personal observations). The diaspores of the three species become covered with thick mucilage once they come in contact with water, which takes about 1–5 min to fully secrete. Dew has been observed to release the secretion of mucilage in these species (author's personal observation).

Seeds of all three species (or the whole calyx in *R. officinalis*) are detached from the mother plant by gravity or by wind, rain or animal disturbance (Güemes and Molero 1993 and authors' personal observations), sometimes followed by secondary seed dispersal by ants (myrmecochory) (Bouman et al. 1992; Arnan et al. 2010). In some occasions, we observed ants collecting fruits, seeds, and ripe calices directly from the plants.

Ant species and their interaction with the target plant species

The research area displayed an average ant nest density of 175 nests per hectare (García-Fayos and Gasque 2006). Six different ant species are present in the study site: *Messor bouvieri*, *M. capitatus*, *Aphaenogaster iberica*, *Formica subrufa*, *Tapinoma nigerrimum*, and *Camponotus sylvaticus*. Of these species, the genus *Messor* (47.8 % of the ant nests in the study area) is the only reputed granivorous ant. *A. iberica* (13 %) is ambiguously considered as granivorous (Azcárate and Peco 2011) and omnivorous (Rey et al. 2002), while *F. subrufa* (8.6 %) and *T. nigerrimum* (26 %) are considered to be nectarivorous and omnivorous (Cavia 1989; Cerdá et al. 1989). *C. sylvaticus* (4.3 %) is recognized as a nectarivorous ant (Retana et al. 1988).

All the ant species except *C. sylvaticus* and *T. nigerrimum* were observed carrying seeds during the observations, indicating that granivorous and omnivorous ant species were actively searching for seeds in the whole area.

To properly interpret the results of our seed survival experiment, we needed to know the strength of the interaction between the ants and the target plant species in our study site. In 2009, we selected and marked 15 nests of ants of *M. bouvieri*, *M. capitatus*, *F. subrufa*, and *A. iberica*, the most frequent ant species collecting seeds in the experimental area, and marked one representative plant of *R. officinalis*, *F. ericoides*, and *F. thymifolia* close to each ant nest. Over the time that the seed removal experiment was performed, we assessed the fruiting status of each plant every 1 or 2 weeks and estimated the amount of seeds available for ants. Additionally, we surveyed seed collection by ants in 10 of the 15 marked ant nests to determine the importance of seeds of the target species as a food source. For this, we counted the number of items that ants transported to individual nests during 10 min periods through the study period, with a total of 32 counts irregularly distributed among the 10 ant nests in function of the coincidence of observation periods with ant activity. Also, we collected the entire waste pile from 14 of the 15 marked nests at different times along the experiment. To analyze the content of the waste piles, about 5 % of dry weight was evaluated completely after mixing the entire waste pile and the relative content of the target plant species was analyzed. The content of the waste pile was then pulled apart visually under the binocular microscope. The separated material was weighted on a precision balance and the relative content of the seeds was evaluated (seed weight/total weight of the waste pile; where total weight includes all vegetal, animal, and mineral materials). The seeds of the target species in our experiment were counted to species level, while the remaining seeds were recorded to the genus or family level when possible.

Seed removal experiments and seed survival analysis

To evaluate the importance of mucilage secretion as a mechanism to escape seed removal by granivorous ants, we performed experiments on removal of loose versus glued seeds (by their own mucilage) of *R. officinalis*, *F. ericoides*, and *F. thymifolia* by ants.

In the spring of 2009, groups of 10 experimental seeds were placed within a radius of 5 m but not closer than 50 cm from the marked ant nests. We placed one group for each studied plant species in the surroundings of ant nests, with a total of 15 replicates per plant species. Half of the seeds in the groups remained dry and loose (control seeds) and the other half of the seeds were placed in distilled water for 20 min until full mucilage secretion was reached. We then placed five control seeds and five moist (mucilaginous) seeds on a flattened patch of bare soil. Petri dish covers (9 cm Ø) were then carefully placed on top and secured with a stone to avoid its displacement. Petri dish covers were provided of two small entrance holes in the side (1 × 1 cm) to permit only the entry of ants. Mucilaginous seeds became glued to the soil surface within 1 h after putting them on the ground. Once mucilaginous seeds had become glued to the ground, they could only be detached when the soil around it was disturbed by animals.

A total of 75 dry and loose (control seeds) and 75 mucilaginous seeds per species were used in the experiment and seed survival was checked every week. Groups of seeds were replaced as soon as control seeds changed the condition from loose to glued to the ground, because of heavy rain, or when Petri dishes got destroyed. The experiments ran from the start to the end of the seed dispersal season of each shrub species (35 days in *R. officinalis*, 84 days in *F. thymifolia*, and 91 days in *F. ericoides*).

The fate of control and glued seeds were individually followed through the experiments and values of 0 and 1 were assigned to represent seed survival and seed removal, respectively. In all trials, the survival time, which served as the response variable, was considered to be the date of the latest survey that the seed was detected.

The Kaplan–Meier estimator (KM) of the survival function was calculated for each of the different seed treatments and plant species. We then checked for differences in survival between the two treatments using the log-rank test (Mantel 1966; Cox 1972). The statistical analysis was made in R statistical package (V. 2.12.2).

Results

Ant species and their interaction with the target plant species

From the inspection we made of items that granivorous ants carried to their nests, we can confirm that ants searched and collected large numbers of seeds of many plant species in the study area (a total of 2,206 counted seeds during the observation times during the study period). About 42.5 % of all observed items were diaspores of the species *R. officinalis*, *F. ericoides*, and *F. thymifolia* (1,109 items in 320 min), and 75.5 % of the dry weight (comparing only the plant remains without soil) in the waste piles of ant nests belonged to propagules of these species.

Large numbers of ripe calices of *R. officinalis* were collected by ants in the first half of April, when nearly 25 % of the items that ants transported to nests were seeds or entire calices of this species (Fig. 1a). In the case of *F. ericoides*, ants were increasingly interested in seeds of this species following the commencement of its fruiting period but never exceeded 10 % of items of its seeds transported to the nests (Fig. 1b). For *F. thymifolia*, ants were found to be transporting high amounts of seeds of this species at the beginning of the fruiting period, counting up to 20 % of the items of seeds carried, and subsequently decreased (Fig. 1c).

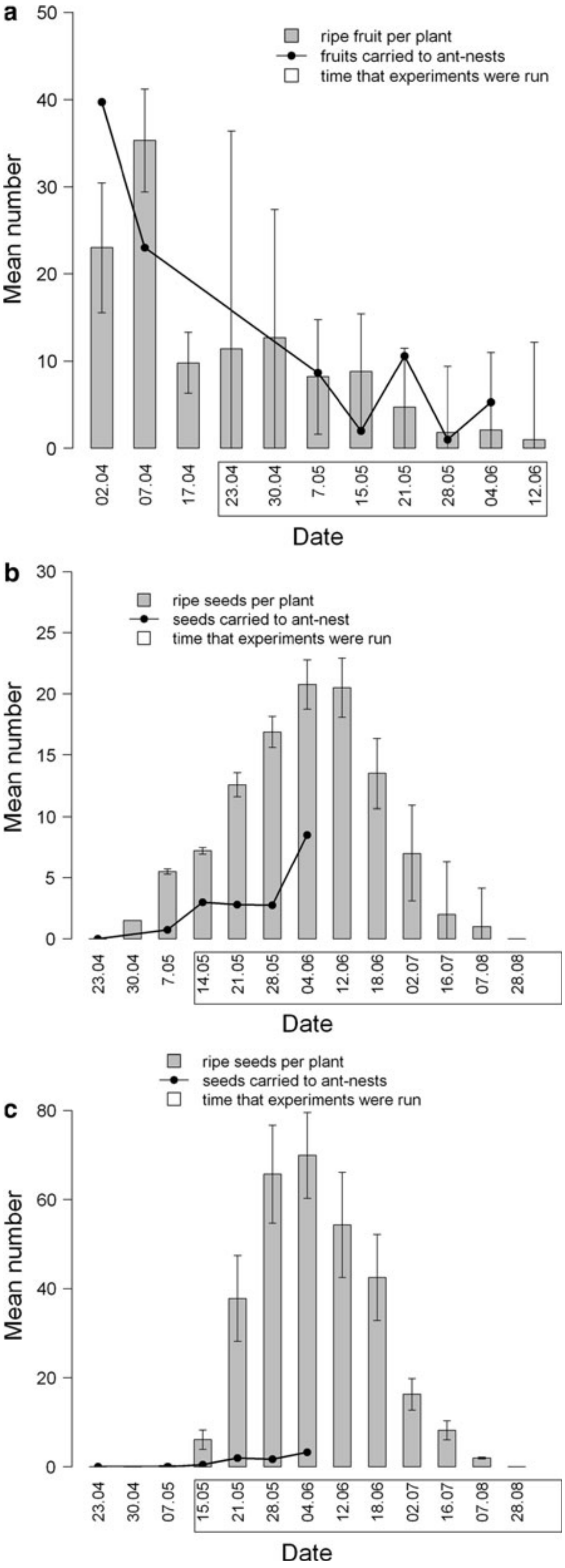
The highest proportion of items in the waste piles of ant nests were entire calices of fruits of Cistaceae, calices and seeds of *R. officinalis*, calices of *T. vulgaris*, and seeds of *S. tenacissima* plus different species of *Fumana* (Fig. 2). Remains of other diaspores found in the waste pile were that of *P. lentiscus*, *Teucrium* sp., and *Thessium humifusum*. Other vegetative plant components and reproductive remains of unknown species were present but are not displayed in the figures.

Seed removal experiments and seed survival analysis

Experimental seeds of *R. officinalis* were offered to ants at the end of the fruiting period of this species (Fig. 1a). In the case of *F. ericoides*, experimental seeds were offered to ants from the 3rd week in which ripe fruits were observed in the field (Fig. 1b) and in *F. thymifolia* the experiment started in the 1st week in which ripe fruits were counted (Fig. 1c).

Seeds that were glued to the ground with their own mucilage survived significantly longer to removal by ants than control (dry and loose) seeds in all three studied species (Fig. 3a–c) and the differences were significant in all the species.

Control seeds of *R. officinalis* were predated strongly in the 1st week that the experiment started and they reached a survival probability of 2 % after 7 days and 0 % after 35 days. Glued seeds were significantly less predated, with a survival probability of 84 % after 7 days, and still 54 % of probability of



◀ **Fig. 1** Ripe fruit (*R. officinalis* with 1–4 seeds per fruit) and seed availability scores in an average of 15 plants, with mean number of seeds carried by ants to nests in four counts of 10 min and time that fruits and seeds were offered in trial experiments to ants over the studied time period for: **a** *R. officinalis*; **b** *F. ericoides*; and **c** *F. thymifolia*

survival after 35 days of exposure ($\chi^2 = 125$, $p < 0.00001$, Fig. 3a).

Control seeds of *F. ericoides* reached a 57 % survival probability after 7 days and a minimum of 13 % after 91 days, while glued seeds showed a significantly higher survival probability, with 90 % of seeds surviving after 7 days and a 71 % survival probability after 91 days ($\chi^2 = 55$, $p < 0.0005$, Fig. 3b).

Seeds of *F. thymifolia* glued to the ground had a survival probability of 88 % after 7 days and remained very high, 68 %, after 84 days of exposure. Control seeds reached a probability of survival of 47 % after 7 days and a minimum 14 % after 84 days of exposure. Differences in seed survival were significant ($\chi^2 = 44.6$, $p < 0.00001$, Fig. 3c).

Discussion

Our experiments showed that seeds of the studied plant species are heavily collected by ants and that mucilage secretion of these diaspores strongly reduced removal by ants, thus favoring a longer persistence in the field. These findings support the idea that granivory by ants is an important factor in seed survival in the study area and that the escape mechanism we addressed here may be relevant for the target plant species.

Inspection of seeds carried by ants and waste piles indicated that seeds of all three species were items of interest for ants. The high proportion of remains of *R. officinalis* in the waste piles and the relatively low proportion of remains of *Fumana* species is consistent with the survival curve of *R. officinalis*, which is removed to a greater extent than the other species (Fig. 3a–c), thus seeming to be of higher interest to ants. Diet and seasonal pattern of harvesting may be explained by relative seed abundance (Briese and Macauley 1981; Hobbs 1985; Willott et al. 2000) and other factors, such as seed coat strength, which could influence ant's preferences. This could explain why seeds of *Rosmarinus* are more likely to be eaten than stronger seeds of *Fumana* species (Rodgerson 1998).

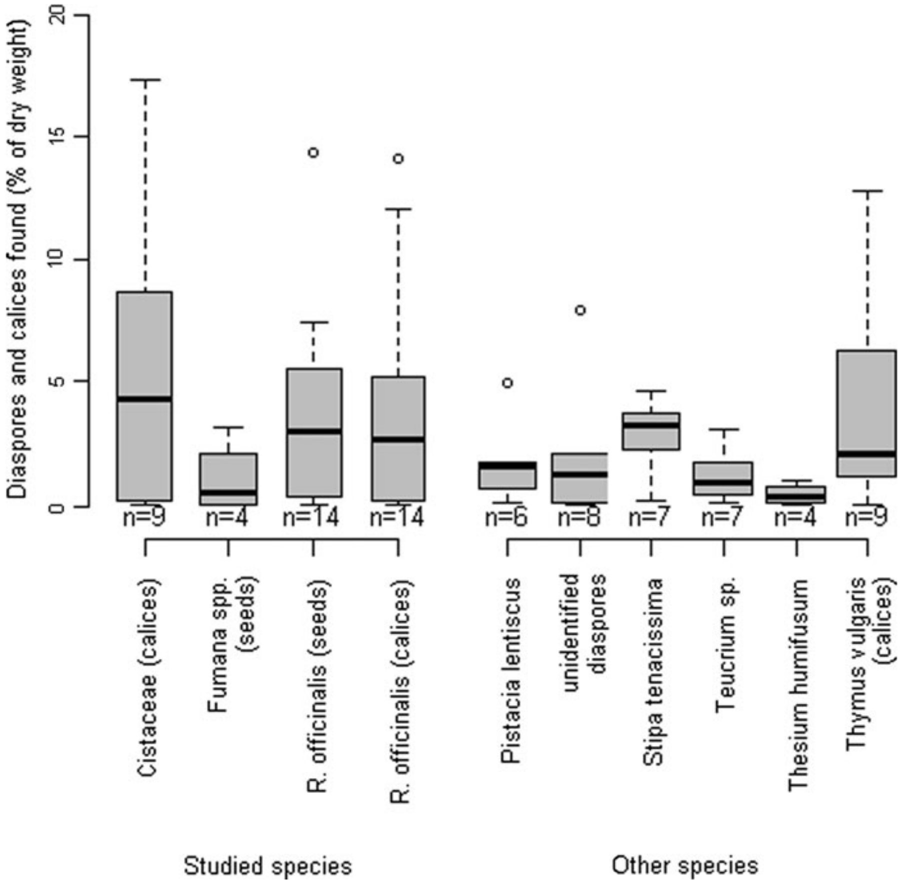
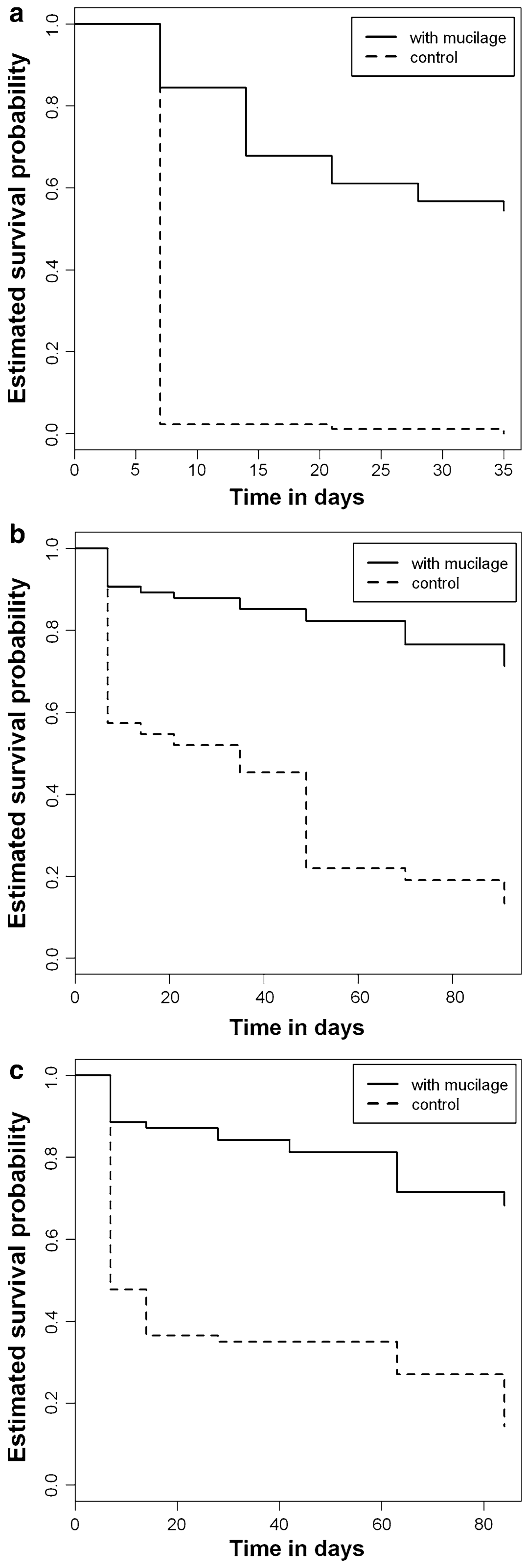


Fig. 2 *Boxplots* of the relative weight of remains of the target species in the waste piles of 14 ant nests in the area where the experiments on seed removal by ants were performed. Values were calculated from dry weight data. Only reproductive remains of plants were displayed (*n* number of ant nests where an item class was found). The *boxplot* displays the smallest and largest value as well as the first quartile, the median, and the third quartile

Still, seeds of the family Cistaceae are of high interest as a food source and are intensely collected in the Mediterranean ecosystem we studied (Bastida and Talavera 2002; Bastida et al. 2009).

More than 50 % of the glued seeds still survived at the end of the experiments but only 0–20 % of the control seeds survived at that time and this strong anti-predatory effect that mucilage has on seed removal is similarly effective in all species. In natural conditions, mucilage is secreted once the seed becomes moistened (Werker 1997) which occurs during rain, fog, or dew (see Methods) and seeds adhere strongly to the soil after drying, thus preventing further removal. Heavy rain events are usually scarce in summer under Mediterranean climate conditions when seeds are released from plants (4.5 days in average in our study area; data from the 2004–2011 period of the Valencia and Castellón meteorological stations, provided by the National Meteorology Agency, Ministerio de Medio Ambiente, http://www.aemet.es/) but dew, fog, and light rain are more frequent meteorological events in Mediterranean semiarid conditions. Morning dew can provide significant amounts of water in dry Mediterranean areas (Kosmas et al. 1998; Kidron 1999; Agami and Berliner 2006), and it frequently occurs during the summer; up to 20 days in late summer (Baier 1966). Summer is usually the season with the lowest fog water yield but still it can make up to an important amount of moisture in comparison with rainfall events, occurring over 25–38 % of the days without rain in the summer months (Estrela et al. 2008).

Granivorous ants can also act as seed dispersers as they accidentally abandon viable seeds on the way to the nest or deposit them in the waste pile (Wolff and Debussche 1999; Retana et al. 2004). Therefore, the view that granivorous ants only harm seeds has been frequently criticized. Removal by ant can have beneficial and detrimental effects, destroying most of the seeds but selectively benefitting some of them (Levey and Byrne 1993; Boyd 1996). In areas where most seeds are consumed, these exceptions can have significant influence on vegetation composition (Dean



◀ **Fig. 3** Estimated survival probability along time of glued and control seeds based on the computed values of the KM estimator for **a** *R. officinalis*; **b** *F. ericoides*; and **c** *F. thymifolia*

and Yeaton 1993; Arnan et al. 2010). It has been reported that up to 16.4 % of the harvested seeds are lost on the track by *M. bouvieri* and that these seeds were not recovered afterward, therefore being effectively dispersed (Retana et al. 2004). Ant-mediated dispersal has been previously reported for *R. officinalis* and *F. ericoides* (Bouman et al. 1992; Arnan et al. 2010), suggesting the importance of removal of seeds by ants for the colonization of open patches. However, some ant species, such as *M. barbarus*, repeatedly find and recover seeds lost on the way to the nest (Detrain and Tasse 2000; Schöning et al. 2004). Whatever the case is, lost seeds on the track to the ant nests can increase their chance to survive if they get glued to the ground, escaping further predation and runoff. This is possible when it coincides with a rainfall event, or more probably, with strong morning dew or fog in summer. This escape strategy seems especially important for *R. officinalis* seeds, as their seeds are heavily predated before and during seed ripening. Often, ants even cut whole ripe calyxes directly from the plant to transport them to the nest, making the loss of single seeds on the track highly probable, as completely ripe seeds easily fall out of the calyx when it is moved (author's personal observation).

At the end of August, we removed the Petri dishes covering the seeds of *F. ericoides* and *F. thymifolia* (only glued seeds remained under them) and followed the fate of the seeds. After the first rain in September, we observed that 50 and 40.8 % of the seeds of *F. ericoides* and *F. thymifolia*, respectively, germinated, in accordance with time of germination reported from field observations of these species and that of *R. officinalis* (Lloret 1998; De Luís et al. 2005). This observation and the results of our experiment of seed removal support the idea that myxospermy plays an important role in determining the spatial pattern of seedling recruitment of these species. So, Arnan et al. (2010) found that overall, 88 % of all patches newly occupied by *F. ericoides* along 3 years were <0.5 m from adult individuals, which agrees with the primary seed dispersal distances of this species. Similarly, López et al. (2003) found that for *R. officinalis*, most of the new recruitments during 2 years were located within 1.75 m around the mother plants. For

F. thymifolia, Jump et al. (2009) studying the within-population genetic structure of this species using amplified fragment length polymorphism, found very limited seed dispersal within the population.

In synthesis, we found that diaspores of the studied plant species were actively searched and collected by ants. Those diaspores that were glued to the ground due to their own mucilage secretion doubled the chance of surviving collection by ant in comparison to the control seeds after several months, thus increasing their chance to establish and providing a mechanism to explain the recruitment patterns of these shrubs.

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