

Effects of harvester ants on seed availability and dispersal of *Lavandula stoechas* subsp. *pedunculata* in a Mediterranean grassland-scrubland mosaic

Ana M. Sánchez^{1,*}, Francisco M. Azcárate² and Begoña Peco²

¹Área de Biodiversidad y Conservación, E.S.C.E.T. Universidad Rey Juan Carlos, C/Tulipán s/n. 28933 Móstoles (Madrid), Spain; ²Departamento de Ecología, Facultad de Ciencias, Universidad Autónoma de Madrid, Campus Cantoblanco 28049 Madrid, Spain; *Author for correspondence (e-mail: ana.sanchez@urjc.es; phone: +34 91 488 82 90; fax: +34 91 664 74 90)

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Abstract

The role of harvester ants in Mediterranean grassland and scrubland has mostly focused on seed consumption. However, recent studies have reported their role as accidental dispersal agents of some of the collected seeds via refuse piles. The objective of this study is to examine the effect of the ant *Messor barbarus* on seed availability and dispersal of one of its major diet components, *Lavandula stoechas* subsp. *pedunculata*, in scrubland, grassland and the ecotones between them. After confirming and quantifying the *Lavandula* contribution to *M. barbarus* diet, we described the spatial and temporal patterns of pre- and post-dispersal seed predation, seed content and seedling occurrence in the refuse piles. Our results show that: (1) *Lavandula* propagules constitute a high proportion of the prey items collected by *M. barbarus*, with particularly intense collection activity in mid-summer, spring and autumn, in decreasing order. (2) Pre-dispersal predation rate was significantly higher in the ecotone than in the scrubland (76% and 13.5% of total seed production lost respectively). (3) Season and propagule type (seed vs. fruit) were the most significant variables explaining the post-dispersal predation probability, which approached 100% of seeds after 48 h in mid-summer. (4) Viable *Lavandula* seeds were found in refuse piles at densities of 0.06–0.2 per g of refuse pile material, or 58.8–207.2 per refuse pile. On the one hand, these results indicate that the ecotones are most affected by *M. barbarus* pre-dispersal consumption, which may locally limit *Lavandula* colonisation. On the other hand, the small proportion of consumed seeds that is dispersed to refuse piles may be relevant at the population level, as this dispersal implies arrival at potentially favourable sites for establishment.

Introduction

The importance of predation by granivorous ants on seed bank dynamics and vegetation in Mediterranean grasslands and scrub communities has been shown in several studies (Cerdan 1989; Wolff and Debussche 1999; Willott et al. 2000). Demo-

graphically, the importance of seed predation is due to its influence on seed availability (Castellanos and Molina 1990; Maron and Simms 1997; Rey and Alcántara 2000). High predation risk does not, however, necessarily imply limitations on the establishment of new individuals. This only exists when the number of available seeds is less than the

number of suitable sites for establishment (Andersen 1989; Eriksson and Ehrlén 1992).

Consumption of fruits and seeds may also imply the dispersal of a proportion of the seeds by the predator (Howe and Smallwood 1982; Van der Pijl 1982; Stiles 1992; Levey and Byrne 1993). Such interactions have been observed between fruit-eating birds and fleshy-fruited Mediterranean shrub species (Herrera 1984, 1995; Jordano 1995), large herbivores and Mediterranean shrubs and grasses (Russi et al. 1992; Malo and Suárez 1995, 1998; Sánchez and Peco 2002) and ants and myrmecochorous species (Milewski and Bond 1982; Bond and Slingsby 1983; Bond et al. 1991).

Although less widely reported, seed predation by granivorous ants may also imply dispersal (dyszoochory). Some predated seeds can accidentally be returned to the soil surface along with other debris in the refuse piles or due to dropped viable seeds along ant trails (Hughes 1991; Dean and Yeaton 1992; Dean et al. 1997; Detrain and Tasse 2000; Retana et al. 2004). Once on the surface, the refuse pile may become a favourable site for establishment, given the lack of competition and the typically higher levels of nutrients at such sites (Dean and Yeaton 1992, 1993a, b; Dean et al. 1997; Cammeraat et al. 2002).

The high frequency of *Lavandula stoechas* subsp. *pedunculata* (Miller) Samp. ex Rozeira (*Labiatae*) - henceforth *Lavandula*- seeds observed in *Messor barbarus* (L.) diet, made us question the extent to which this interaction could be relevant to the regeneration potential of *Lavandula*. These two species are widely distributed on the Iberian Peninsula in areas where the vegetation consists of mosaics of Mediterranean scrubland and grassland on siliceous soils (Azcárate 2003). However, no specific studies have been conducted on the role of predation and dispersal of *Lavandula* seeds by granivorous ants in the dynamics of these systems.

Previous studies (Sánchez and Peco, in prep.) have found high *Lavandula* seed availability in the scrubland, and almost none in the adjacent grassland as a result of the low dispersal range through autochory (Sánchez and Peco 2002). The high density of *M. barbarus* colonies in the ecotones between scrubland and grasslands (Azcárate and Peco 2003) could accentuate seed limitation in the potential expansion area of *Lavandula*, as ants collect seeds from a number of species from both the grassland and the adjacent scrub communities

(Azcárate and Peco 2003). At the same time, *M. barbarus* activity may influence seed dispersal if some of the predated seeds are accidentally returned to the soil surface at points impossible to reach by autochory.

In order to contrast both hypotheses after confirming and quantifying the *Lavandula* contribution to *M. barbarus* diet, we recorded data on: (i) spatial and temporal patterns of pre- and post-dispersal seed predation; (ii) viable seed content in refused piles located in the grassland. We also examined the suitability of these sites for recruitment through the appearance of *Lavandula* seedlings.

Methods

Study area

The research was conducted at the Moncalvillo-Pedrezuela site (Central Spain: 40°38' N, 3°70' E; 2000 ha), an area with continental Mediterranean climate (altitude 900 m a.s.l.; mean annual temperature 13.2 °C; mean annual rainfall 540 mm). The substrate consists of shallow acid soils on gneiss. The vegetation is a mosaic of grasslands and scrubland with scattered *Quercus ilex* subsp. *ballota* (Desf.) Samp. and *Juniperus oxycedrus* L. subsp. *badia* (H.Gay) Debeaux in the rockiest areas. All measurements were recorded in a representative 5 ha area including the three main habitats: scrubland, grassland and ecotones between them. We define the ecotone as the area in which the grassland is mixed with some *Lavandula* plants, while the grassland is the area in which only the herbaceous community is present.

The predominant scrub species is *Lavandula stoechas* subsp. *pedunculata*, found in almost monospecific patches with an average density of 1.89 individuals/m² (S.D.=0.65). *Lavandula* is a Mediterranean seeder shrub (Herrera 1992), distributed through Iberia and North Africa. "Seeds" are actually mericarps, with average mass 0.91 mg, long-axis length 1.79 mm, and no dispersal structures (Azcárate et al. 2002). Prior to dispersal, mericarps temporarily persist inside the calyx, henceforth "fruit".

Messor barbarus is the predominant granivorous ant in the ecotone areas between scrubland and grassland. *Messor bouvieri* (Bond.) colonies have

also been recorded in the study area, but the activity of this species is restricted to scrub communities. The density of *M. barbarus* nest-holes varies between 200 and 300 per hectare, concentrated on the ecotones and adjacent scrub areas (Azcárate and Peco 2003). At distances higher than fifty meters from the ecotone, *M. barbarus* is almost absent (Azcárate 2003). These nest-holes are easily detected by the conspicuous trails leading to them (López et al. 1993, 1994) and refuse piles measuring up to 1 m in diameter (Cerdan 1989).

Study design

To study the importance of *Lavandula* in the *M. barbarus* diet, 34 samples were taken in 1997 and stratified temporally in accordance with the relative importance of each season in the annual harvesting activity (Azcárate 2003): 11 in spring (April–May), 10 in early summer (July), 10 in late summer (August) and 3 in autumn (October). Each sample consisted of an average of 41 prey items carried by the ants, taken from independent colonies during periods of 2–3 min. The percentage of *Lavandula* mericarps, fruits and infrutescences were calculated for every sample.

To quantify pre-dispersal predation two 100 m × 0.5 m wide transects were established, one per habitat type: scrubland vs. ecotone. Pre-dispersal predation was recorded for all *Lavandula* plants intercepted in each transect ($n=73$ in the scrubland; $n=11$ in the ecotone). We noted whether the plants displayed signs of predation, and if so, the proportion of infrutescences cut by workers on a semi-quantitative scale: 1 (1–25%), 2 (26–50%), 3 (51–75%) and 4 (76–100%). Average values for each habitat type were obtained using the central percentages for each interval (12.5; 37.5; 62.5; 87.5%). Data were collected at the end of September 1999 after most of the seed predation by harvester ants had concluded. The percentages of harvested infrutescences in scrubland and ecotone were compared using the Mann-Whitney *U*-test.

To assess post-dispersal predation artificial bait consisting of 5.5 cm diameter Petri dishes filled with 50 *Lavandula* seeds / fruits were used to evaluate the spatio-temporal pattern of post-dispersal predation. Holes were cut on opposite sides of the dishes

to facilitate the passage of ants. All dishes were protected by wire mesh cages (14 × 14 × 2.5 cm) with 4 mm spacing to impede predation by vertebrates and larger invertebrates (Hulme 1994; Predavec 1997; Azcárate and Peco 2003). The experiment was performed under good weather conditions in order to avoid rain and wind effects over the Petri dishes. This type of bait does not facilitate information on absolute predation rates, but does provide a relative measurement that permits comparisons between different experimental treatments.

We recorded 324 independent observations, 108 for each season: early summer (July); late summer (August) and autumn (September). Two additional factors, prey type (seeds/fruits) and habitat type (scrubland/grassland/ecotone), were included in the design. Thus, each combination of season, prey type and habitat type was represented by 18 independent observations. The baits were randomly distributed in each habitat type, keeping a minimum distance of 5 m between dishes. The bait was set at midday and checked 24 and 48 h afterwards to note whether the dish had been predated (1) or not (0). We considered baits were predated if it was empty. This is due to the mass recruitment strategy followed by *M. barbarus* when they find a concentrated source of food.

Logistic regression models were fitted to the data to evaluate the effect of the different variables on the predation probability after 24 and 48 h. The explanatory variables were transformed into dummy variables. A step-wise backward regression model was used as this is more appropriate when dummy variables are used (Zar 1996). The SPSS computer package was used for the analyses (SPSS Inc. 1999).

To evaluate dyszoochory, in September 1997 and 1999, material was collected from 9 and 20 refuse piles respectively from different colonies located in the scrubland-grassland ecotone, the habitat where scrub colonization could potentially occur. The collected material was dried and weighed. After homogenisation, a 10 g extract was taken from each refuse pile and subjected to two years of greenhouse cultivation to ascertain the viable seed content (see Traba et al. 1998 for details on cultivation).

We also recorded the presence of *Lavandula* seedlings in 20 × 20 cm quadrats set on 29 refuse piles (9 in 1997 and 20 in 1999), selected using the

same criteria as above, and in another 29 adjacent areas. The refuse piles were marked with nails at the end of the summer and visited in December after the autumn germination period, and again in May to check for possible spring germinations.

Results

Lavandula propagules formed a high proportion of the prey items collected by *M. barbarus* (Table 1). The ants mainly collected *Lavandula* fruits and seeds. These propagules were harvested throughout the year except in June, with particularly intense activity in mid-summer (after 15 July), spring and autumn, in decreasing order.

Symptoms of pre-dispersal predation were only found in 19 individuals in the scrubland transect (26%), in contrast with the 100% recorded in the ecotone (Figure 1). Predation intensity as a proportion of infrutescences cut by ants was significantly higher in the ecotone ($U = 51.5$; $p < 0.0001$), indicating a pre-dispersal predation loss of 76% and 13.5% of total seed production in ecotones and scrubland, respectively.

The overall predation probabilities were very high, reaching values close to 100% for bait predated after 48 h, especially in July and August (Figure 2). The models for both the 24 and 48 hour periods (Table 2) coincide in the importance of the month and bait type as the most significant variables explaining the predation probability. Differences between habitats were not observed.

The average mass of the material deposited in the refuse piles was 1031 ± 622 g and the average occupied area was 1798 ± 842 cm². In 1997 and 1999, 55% and 65% of the samples, respectively, contained viable *Lavandula* seed. Greenhouse sample cultivation shown an average of 0.06 and 0.2 viable *Lavandula* seeds per g of refuse pile

material, which amounts to 58.8 and 207.2 viable seeds per refuse pile, respectively for the two study years. Only one seedling was found in the refuse piles and no seedlings appeared in the adjacent areas.

Discussion

This study confirms the existence of at least a close quantitative interaction between *Lavandula* and *M. barbarus*. A remarkably high proportion of *Lavandula* propagules was observed in the harvester ant diet through most of the year. Maximum values were reached in mid-summer, coinciding with the ripening of *Lavandula* fruits. In early summer, however, ants concentrated on other prey types to benefit from the availability peak of herbaceous seeds (Azcárate et al. 2002). Spring consumption is possibly explained by the considerable amount of non-dispersed seeds remaining in the infrutescence (personal observation).

M. barbarus must be regarded as a significant if not primary seed removal agent. Our data show that harvester ants are responsible for very high seed losses both before and after dispersal. Pre-dispersal seed predation is particularly intense in the ecotones, which can be explained by the higher density of *M. barbarus* colonies in these areas (Azcárate and Peco 2003) and the lower seed availability. Post-dispersal predation data, however, do not reveal any differences between the habitat types. This can be explained by the fact that ants can collect seeds as far as thirty meters away from the nest entrance (Cerdan 1989). It also should be noted that the bait used was very attractive and easy to collect, and that 24 h was enough time for the bait to be located, even in habitats where foraging intensity was not very

Table 1. Proportions (%) of the total prey collected by *Messor barbarus* of each of the possible propagule types produced by *Lavandula stoechas* subsp. *pedunculata*, throughout the year.

	Spring		Early summer		Mid summer		Autumn	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Seeds	8.24	2.7	0.00	0.0	15.98	6.2	18.66	2.2
Fruits	25.67	8.2	1.63	1.6	24.12	6.7	5.88	2.7
Infrutescences	0.71	0.5	0.00	0.0	5.19	1.7	0.00	0.0
Total	34.62	10.0	1.63	1.6	45.29	9.2	24.54	4.8

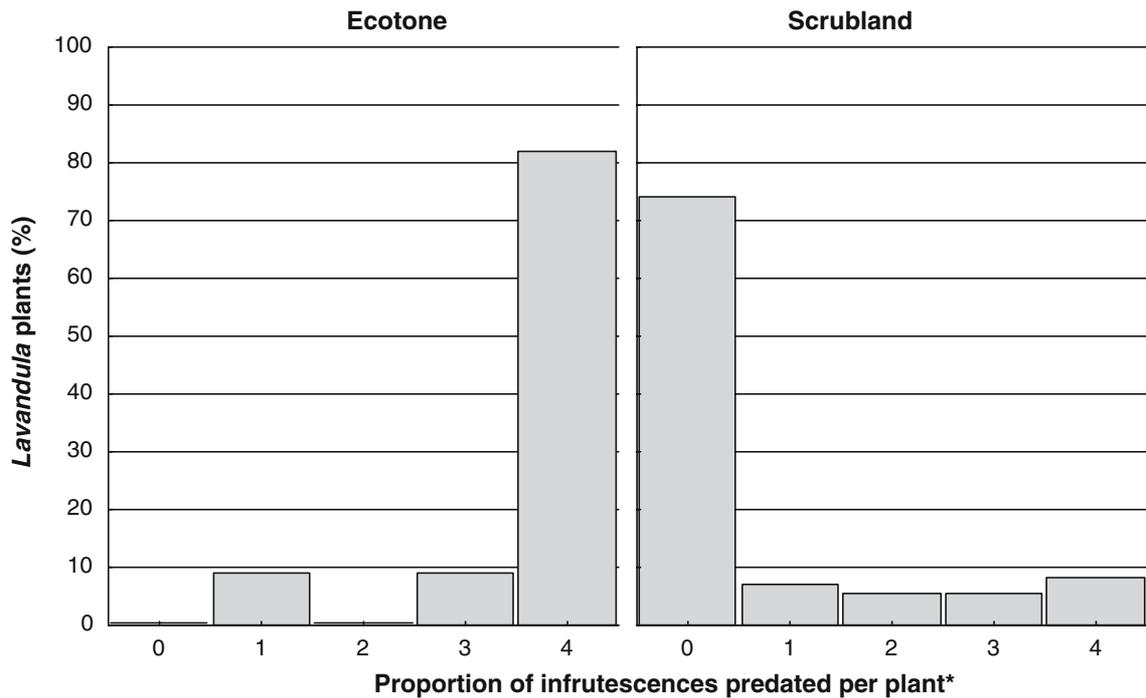


Figure 1. Percentage of *Lavandula stoechas* subsp. *pedunculata* plants showing different intensity of predispersal predation indicated by the proportion of infructescences predated by *Messor barbarus* workers per plant. *(1: 1–25%, 2: 26–50%, 3: 51–75% and 4: 76–100%).

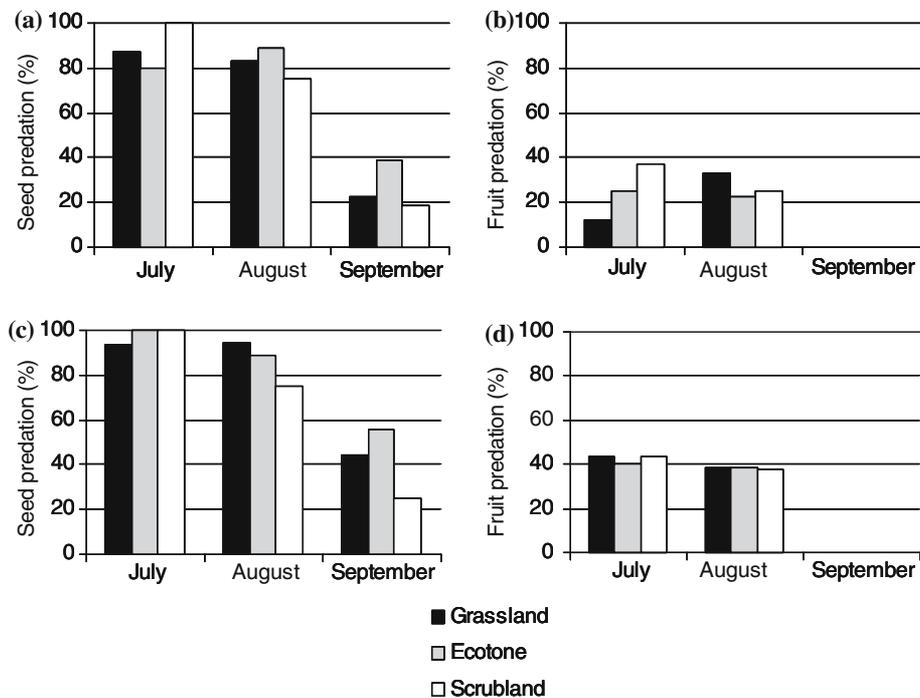


Figure 2. *Lavandula stoechas* subsp. *pedunculata* fruit and seed post-dispersal predation percentages observed after 24 (a and b) and 48 (c and d) hours in the field, over the study period and in the various analysed habitats.

Table 2. Models obtained to explain the probability of *Lavandula stoechas* subsp. *pedunculata* seed and fruit post-dispersal predation by *Messor barbarus* for 24 h and 48 h periods.

Variables included in models	24 h		48 h	
	$\chi^2 = 154.92^{**}$ % = 81.9 B (St. Error)	df = 3 $r^2 = 0.53$ Wald (df)	$\chi^2 = 162.81^{**}$ % = 76.7 B (St. Error)	df = 3 $r^2 = 0.54$ Wald (df)
Constant	-3.99 (0.4)	82.06** (1)	-3.55 (0.5)	61.28** (1)
Season (1)	2.99 (0.4)	46.17** (1)	3.39 (0.5)	50.00** (1)
Season (2)	2.86 (0.4)	43.34** (1)	2.86 (0.5)	39.25** (1)
Bait (1)	2.93 (0.4)	71.18** (1)	3.15 (0.4)	60.44** (1)

The accuracy of the models is indicated by the percentage of correct predictions (%) and the variance explained using the Nagelkerke R-squared (r^2). *B* values are the model coefficients and the degree of significance of the model and the variables are indicated using asterisks in the χ^2 and Wald statistics, respectively: * < 0.05; ** < 0.001.

high. However, shorter observation periods should be tested in order to confirm the absence of differences among habitats. In addition, we can not discard a possible interference of *M. bouvieri* in the scrubland. However, its effect is not likely to be relevant, as this species is much less abundant than *M. barbarus* in the study area, both in terms of number of colonies and number of workers (Azcárate 2003; Azcárate and Peco 2003).

On the contrary, the post-dispersal experiment was capable of detecting seasonal and bait-type differences. Predation declined dramatically in the second half of September, probably a reflection of the gradual reduction in the ant's activity period (Azcárate 2003). Between the bait types, *Lavandula* seeds triggered a much more intense predation than fruits. This preference may be a consequence of the shorter time needed to transport the seeds, which are much lighter than the fruits, despite the higher nutritional value of the latter. Previous studies seem to show that harvester ants prioritise time reduction in relation to the net energy gain per prey (Morehead and Feener 1988; Reyes-López and Fernández-Haeger 2002). However, more research is needed to clarify the factors affecting prey preference in harvester ants.

Predation probabilities as high as those observed in our area have also been found in other studies (Harrington and Driver 1995; Predavec 1997). However, high predation risk does not necessarily have demographic consequences. The key lies in the relationship between number of available seeds and favourable sites after seed predation by ants (Andersen 1989). In the study area this largely varies with habitat. A high abundance of both seeds and seedlings was found

in scrubland, although survival data suggest a lack of favourable sites. In contrast, seed availability declines dramatically in the ecotone due to the lack of efficient dispersal mechanisms (Sánchez y Peco, in prep; Sánchez and Peco 2002). Thus, the activity of *M. barbarus* as a predator does not necessarily have demographic consequences inside the *Lavandula* patches. However at the ecotones, most heavily affected by *M. barbarus* activity, ant seed predation could intensify seed scarcity and thus limit the *Lavandula* colonisation potential. Further experimental work should be done to ascertain the real power of this negative interaction.

In order to evaluate the demographic consequences of this interaction, it is also necessary to add the implications resulting from the role of *M. barbarus* as a seed dispersal agent. This positive relationship may be highly relevant for *Lavandula* at the population level. The results of this study show that consumption of *Lavandula* seeds by *M. barbarus* is accompanied by the accidental dispersal of a considerable number of viable seeds discarded in the refuse piles (Hughes 1991; Dean and Yeaton 1992; Dean et al. 1997). Although the distance involved in this type of dispersal is limited, it enables the seeds to reach the grassland and generate densities that are impossible via autochory (Sánchez and Peco 2002). This dual role of *Messor* in Mediterranean environments has been previously suggested for other species (Retana et al. 2004). Thus the idea that these ants are merely predators which only interact with plants antagonistically should be reconsidered.

The potential importance of this dispersal depends on the degree to which the *Lavandula*

seeds are able to establish and grow in these locations (Schupp 1993, 1995). Refuse piles may be highly suitable for *Lavandula* growth, especially after abandonment given the negligible level of occupation here, the open, well-aerated soil and the higher nutrient availability (Dean and Yeaton 1992, 1993a; Cammeraat et al. 2002; Azcárate 2003). In other studies, seedlings of various species have been shown to become established in refuse piles and colony entrance tunnels (Danin and Yom-Tov 1990; Bossard 1991; Dean and Yeaton 1993b; Dean et al. 1997; MacMahon et al. 2000). In the case of *Lavandula*, although the data on seed dispersal are convincing, there is still no evidence of seedling establishment. A broader study, both spatially and temporally, should be necessary to rule out recruitment, especially in relation to disturbance episodes and in above-average rainy summers.

In summary, the results demonstrate the previously unknown dual role of *M. barbarus* harvesting activity on *Lavandula* and the importance of this interaction for both sides. *Lavandula* seeds are a fundamental part of *M. barbarus* diet, and for *Lavandula*, pre-dispersal predation involves the loss of a high proportion of seed production. The intensity and importance of the relationship is much higher in the ecotones where the presence of ant nests could therefore facilitate the establishment of *Lavandula* individuals in the grassland domain.

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