

Original article

Assessing ant seed predation in threatened plants: a case study

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Abstract

Erodium paularense is a threatened plant species that is subject to seed predation by the granivorous ant *Messor capitatus*. In this paper we assessed the intensity and pattern of ant seed predation and looked for possible adaptive strategies at the seed and plant levels to cope with this predation. Seed predation was estimated in 1997 and 1998 at the population level by comparing total seed production and ant consumption, assessed by counting seed hulls in refuse piles. According to this method, ant seed predation ranged between 18% and 28%. A more detailed and direct assessment conducted in 1997 raised this estimate to 43%. In this assessment spatial and temporal patterns of seed predation by ants were studied by mapping all nest entrances in the studied area and marking the mature fruits of 109 reproductive plants with a specific colour code throughout the seed dispersal period. Intact fruit coats were later recovered from the refuse piles, and their mother plants and time of dispersal were identified. Seeds dispersed at the end of the dispersal period had a greater probability of escaping from ant seed predation. Similarly, in plants with late dispersal a greater percentage of seeds escaped from ant predation. Optimum dispersal time coincided with the maximum activity of granivorous ants because, at this time, ants focused their harvest on other plant species of the community. It was also observed that within-individual seed dispersal asynchrony minimised seed predation. From a conservation perspective, results show that the granivorous ant–plant interaction cannot be assessed in isolation and that the intensity of its effects basically depends on the seed dispersal pattern of the other members of the plant community. Furthermore, this threat must be assessed by considering the overall situation of the target population. Thus, in *E. paularense*, the strong limitation of safe-sites for seedling establishment reduces the importance of seed predation.

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1. Introduction

Seed predation by ants has rarely been considered in assessing the conservation status of endangered plant populations. However, the impact of seed predation on population dynamics has been intensively studied (Harper et al., 1970; Janzen, 1971; Brown and Human, 1997; Howe and Brown, 2000, 2001; MacMahon et al., 2000), and consequently recognised as an important factor in shaping the structure and composition of plant communities (Brown et al., 1979; Louda, 1982; Heske et al., 1993; Hulme, 1997, 1998).

Among seed predators, harvester ants are considered primary seed consumers in low nutrient or dry environments (Morton, 1985; Beattie and Hughes, 2002), and their forag-

ing behaviour is known as a major determinant of both community and population attributes (Kunin, 1994; Hulme and Benkman, 2002). In fact, ant foraging can influence the relative recruitment rates of preferred and rejected species (Reichman, 1979; Crist and MacMahon, 1992; Kunin, 1994).

Seed predation by harvester ants becomes an especially relevant matter for endangered plant populations when relatively high predation rates have been previously reported (Crawley, 1992). Ant granivory may exert selective pressure on small plant populations and condition their viability. Some authors have hypothesised that seed aggregation may increase the removal rate by ants (Hughes and Westoby, 1990; Gorb and Gorb, 2000). According to this, high within-population dispersal synchrony, resulting in high seed densities, could become detrimental. We hypothesised that natural selection may have shaped dispersal phenology in two different ways: 1) Maximising the probability of a seed escaping from ant

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predation (seed perspective). Those genotypes whose time of seed dispersal does not coincide with the peak activity of seed predators may have a greater chance of escaping from predation. This implies that the new seed genotypes exert certain control in the ripening process that complement plant maternal effects (Roach and Wulff, 1987). 2) Maximising the number of seeds per plant that escape from ant predation, both in absolute and relative terms (plant perspective) (Moore, 1978; De Steven, 1983).

In the course of a long-term study on the reproductive biology and demographic dynamics of the rare plant *Erodium paularense* Fern. Gonz. and Izco (Geraniaceae) (González-Benito et al., 1995; Albert et al., 2001a; Albert et al., 2001b; Albert et al., 2004), we observed significant seed predation rates by *Messor capitatus* ants, the only harvester ant found in the populations (X. Espadaler and C. Gómez, personal communication). However, population viability analyses based on more than 10 years of monitoring suggest that local populations are relatively stable (Albert et al., 2004) in spite of the intense and constant removal of viable seeds. We considered that these populations might have evolved mechanisms to cope with this constant recruitment limitation. Therefore, we built models to determine the factors that affect the probability of a seed escaping from predation, and the number and the percentage of non-predated seeds per plant.

Thus, our specific questions were: a) What is the level of ant seed predation in *E. paularense*? b) What is the spatial and temporal pattern of this ant seed predation? c) Have seeds and plants adopted any strategies to escape from ant seed predation? and d) What implications can be derived for the conservation of this plant species?

2. Materials and methods

2.1. Study species

E. paularense Fern. Gonz. and Izco is an endangered woody rosulate that grows in the Sistema Central in Spain on dolomitic and andesitic rock outcrops and in nearby shallow soils. It is listed in Annex II and Annex IV of the European Community Habitats and Species Directive (European Community, 1992) and has been classified as “Endangered” (EN) (Albert et al., 2003) according to IUCN categories (IUCN, 2001). Plants produce very few viable seeds due to the operation of a partial self-incompatibility system and other limiting factors such as relatively low levels of flowering synchrony and resource limitation (González-Benito et al., 1995; Albert et al., 2001a). Fruits (schizocarps) are composed of five one-seeded mericarps. Mericarp dispersal occurs by a hygroscopic mechanism by which they fall to the ground within a 2-m range from the mother plant (M.J. Albert, personal observation). Further limiting factors for the viability of its populations include adequate microsite limitation and low seedling survival (Albert et al., 2004).

The study was conducted in Valle de Lozoya, Madrid, Spain (Population II of González-Benito et al., 1995).

2.2. Estimation of total seed production

In 1997 and 1998 all individuals of the population were censused. Each year plant size was measured through the maximum diameter of rosette cluster in a sample of 300 plants. Individuals were then ascribed to one of eight size classes used to structure the population (Table 1). Total number of individuals in each class was calculated from this population structure and the total number of individuals censused. When the mericarps are dispersed, the axial column of schizocarps remains on the plant. Based on this knowledge, total number of fruits was measured at the end of each fruiting period in a random sample of 200 plants.

A GLM model with Poisson distribution and a logarithmic link-function was built in order to estimate fruit production per plant as a function of plant size (Nicholls, 1989; Guisan and Zimmerman, 2000). Consequently, fruit production for an average individual of each size class was estimated. Total fruit production in the population was calculated by multiplying the total number of plants in each size class by its corresponding fruit production, and adding the results from all size classes. Each year the number of viable seeds per fruit was estimated from a sample of 110 fruits randomly collected from the different size classes throughout the whole population. Fruits were opened at the laboratory and the number of brownish coloured and turgid seeds were counted. The viability of these seeds had been previously assessed (Pérez-García et al., 1995). Finally, total seed production was obtained by multiplying total fruit production by the average number of seeds per fruit for each year.

2.3. Estimation of seed predation by ants

Seed predation by *M. capitatus* at the whole population was estimated by counting *E. paularense* mericarps in the waste from all ant nests within the geographical range of the plant population, and those found up to 10 m away. Waste was accumulated on piles of discarded materials removed by ants from their nests (Traniello, 1989). All *M. capitatus* nests ($n = 21$) were recorded and waste accumulated on the refuse piles was collected at 20-day intervals from the beginning of seed dispersal in early May until the end of September. Existing accumulated waste was eliminated before the beginning

Table 1
Estimated number of fruits per plant within each size class (mean \pm S.D.) using GLM Poisson regressions

Size class (cm)	Number of fruits 1997 ^a	Number of fruits 1998 ^b
<6	4.24 \pm 0.45	1.98 \pm 0.29
6–10	6.97 \pm 1.03	3.58 \pm 0.65
11–15	11.99 \pm 1.82	6.62 \pm 1.17
16–20	20.31 \pm 3.11	11.78 \pm 2.30
21–25	36.99 \pm 6.21	23.01 \pm 4.29
26–30	62.30 \pm 10.81	38.28 \pm 6.70
31–35	107.09 \pm 20.18	88.79 \pm 20.33
>35	261.57 \pm 109.52	133.08 \pm 0.00

^a $\text{Ln}(\text{fruits}) = 0.8728 + 0.0980 \times \text{size}$. $N = 300$.

^b $\text{Ln}(\text{fruits}) = 0.2063 + 0.1099 \times \text{size}$. $N = 300$.

of seed dispersal, in order to avoid counts for seeds stored in the previous season. Although harvester ants may reject plant material out of the nest after September, we had previously observed that this fraction is negligible (A. Escudero, personal observation) and the period studied was representative to estimate seeds collected by ants. All *E. paularense* mericarp coats were manually separated from each refuse pile and counted. Mericarp coats and the rest of nest waste were dried at 60 °C for 48 h and then weighed separately in order to estimate the relative importance of *E. paularense* seeds as ant food resource. The foraging behaviour of *M. capitatus* was observed at the nest entrance at the peak of ant daily activity for a total of 9 h during 7 consecutive days.

2.4. Seedling recruitment and soil seed bank

In the autumn of the two studied years, seedling emergence was surveyed in the whole population. Seedlings were tagged and growth was measured as the number of developed leaves. Growth and survival were regularly surveyed at 15–30-day intervals throughout the following year. Twenty soil samples (7 × 5 × 3 cm) were randomly taken at the end of the winter to evaluate the existence and size of a permanent soil seed bank. Seed germination had been previously studied in the laboratory, obtaining rates of 100% at alternating temperatures of 15/25 °C (Pérez-García et al., 1995).

2.5. Spatial and temporal predation patterns

In the first year of study, a more accurate method was used in order to determine which factors affect seed predation. The 21 *M. capitatus* nest entrances found in the population were mapped. One hundred and nine reproductive plants (over 4-cm diameter, which is the minimum size for flowering, Albert et al., 2001a) were randomly selected, tagged and mapped. Plants were monitored every 2–5 days throughout the seed dispersal period, for a total of eight dates (T1–T8). At each census, all mature mericarps that were brownish coloured, turgid and ready for dispersal were carefully marked with nail polish using the tip of a needle, following a three-colour code. The first two markings were used to identify the mother plant, and the third was used to register the dispersal date. We had previously observed that this polish had no impact on seed dispersal and seed predation rates (M.J. Albert, personal observation). Nest refuse piles were collected at 20-day intervals and all *E. paularense* mericarps in each pile were counted. Marked mericarps were identified and their mother plant, dispersal date and the ant nest where they had been found were registered. At the end of the experiment, a total of 924 mericarps had been marked. Obviously, this technique allows a much more real and detailed estimation of seed predation of the target plants.

In order to know how long the seeds were stored in the nests before consumption, we calculated the time lag between the dispersal of a mericarp and the appearance of the mericarp coat in the refuse pile. Time lags were grouped in 20-day

periods (interval of refuse pile collection) and total number of seeds within each time lag was calculated.

2.6. Numerical analyses

2.6.1. Seed perspective

In order to model the probability of a seed escaping from ant predation, we considered a group of factors that may affect this variable: (a) total seed production of each mother plant as the sum of seeds marked on each plant throughout the monitoring period, (b) total seed production in the neighbourhood as the sum of total seed production from all marked plants in the neighbourhood, (c) dispersal date as eight complementary dummy variables (i.e. a 0, 1 variable), and (d) total number of dispersed seeds at each dispersal date in the neighbourhood. Considering the estimated seed dispersal range of this species, neighbourhood was defined to include all plants present within a 1.5 m radius of the target mother plant.

2.6.2. Plant perspective

In this case the modelled variables were the number and percentage of non-predated seeds per plant. The independent variables included were: (a) total seed production of the mother plant, (b) total seed production in the neighbourhood, (c) dispersal time, as the time at which the highest number of seeds was dispersed by the mother plant, and (d) dispersal synchrony. This last variable is a measurement of the degree of dispersal overlapping of the mother plant with the rest of plants in the neighbourhood. The following function, applied by Albert et al. (2001a) for flowering synchrony was used:

$$S_i = \frac{1}{n-1} \sum_{j=1}^{n-1} \frac{a_{ij}}{b_{ij}}$$

where n is the number of plants, a_{ij} is the number of days on which j and i individuals simultaneously disperse seeds, and b_{ij} is the number of days on which at least one of them (j and/or i) disperses seeds. This index ranges from 0, when there is no synchrony, to 1 when dispersal synchrony is complete.

Plant size and duration of dispersal period were also considered but were not included in the models due to multicollinearity problems (Variance Inflation Factor over 10). Spearman correlations (due to lack of normality for the data) were obtained instead for these variables to assess their effect on the number of non-predated seeds.

2.6.3. Generalised linear models

Generalised linear models (GLM, McCullagh and Nelder, 1999) were built using S-PLUS 2000 (MathSoft, 1999). We chose GLMs rather than linear regressions because they can use a greater number of distribution classes for the response variable and non-constant variance functions. Based on deviance reduction criteria (McCullagh and Nelder, 1999; Guisan and Zimmerman, 2000), a binomial response with a logit link-function was selected for the seed perspective, whereas a

Gaussian response with an identity link-function was selected for the plant perspective. Significant terms were identified using a stepwise addition of terms to the null model based on the magnitude of the Cp statistic (Spector, 1994) until no additional terms improved the model. Regression coefficients were tested for significance by *t*-tests and randomisation due to the possible lack of independence of data. χ^2 tests were also conducted to determine if selected predictors explained a significant fraction of the deviance (Guisan et al., 2002).

Reduced models were compared to the saturated model. Change in deviance between each pair of models was assessed using an *F*-test because all preliminary models were nested. Adjusted D^2 , which is equivalent to adjusted r^2 in LS models, followed Guisan and Zimmerman (2000).

3. Results

3.1. Seed production in the population

The total number of individuals in the population was 3574 in 1997 and 3002 in 1998. In both years, fruit production increased with plant size (Table 1). Plant size was a good predictor of per plant fruit production for both years (1997 $D^2 = 0.55$, 1998 $D^2 = 0.37$; $P < 0.001$). Mean number of fruits per plant for each size class was higher in 1997 than in 1998 (Table 1). Thus, total estimated number of fruits produced in the population were 100,785 and 31,016 in 1997 and 1998, respectively.

Number of viable seeds per fruit was 0.27 ± 0.64 (range 0.00–4.00, $n = 110$) in 1997 and 0.49 ± 1.09 (range 0.00–5.00, $n = 110$) in 1998. Thus, estimated seed production in the whole population was 27,212 and 15,198 seeds per year, respectively.

3.2. Seed predation by ants, seedling recruitment and soil seed bank

Observations on foraging behaviour showed that *M. capitatus* individuals only harvested mericarps with fully-developed viable seeds, whereas mericarps with aborted seeds and seedless mericarps were rejected. All intact mericarp coats found at the refuse piles were then assumed to have contained one viable seed. Only three unopened mericarps with the corresponding seed inside were found on the refuse piles in 1997, whereas in 1998 all mericarps lacked their seeds.

The number of mericarp coats found on the refuse piles indicated that *M. capitatus* harvested at least 7554 seeds in 1997 (27.76% of total seed production) and at least 2680 seeds in 1998 (17.63% of total seed production). However, considering only the mericarps that were marked with nail polish in 1997, 401 mericarp coats out of 924 marked mericarps were recovered from the waste dumps (Fig. 1). This direct and more accurate estimation shows a higher seed predation incidence (43.40%).

Most predated mericarps (86.10%) appeared in the refuse piles within 2 months after dispersal (Fig. 2), indicating that ants consumed most *E. paularense* seeds within this period.

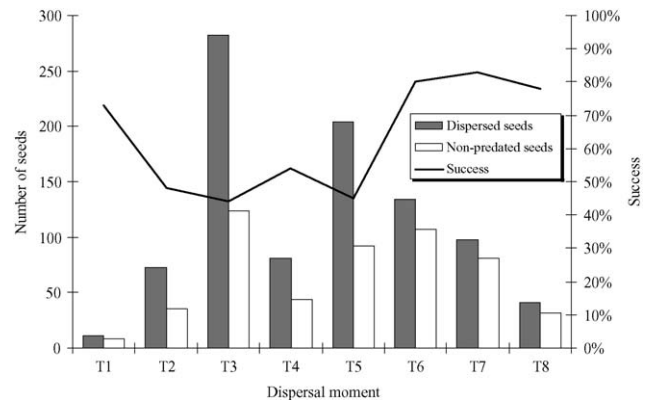


Fig. 1. Number of dispersed and non-predated seeds, and percentage success of *E. paularense* seeds ($\frac{\text{non-predated seeds}}{\text{predated seeds}} \times 100$) on different seed dispersal dates (T1–T8) throughout the reproductive season. T1 = 30-April, T2 = 8-May, T3 = 12-May, T4 = 14-May, T5 = 20-May, T6 = 24-May, T7 = 27-May, T8 = 30-May-1997.

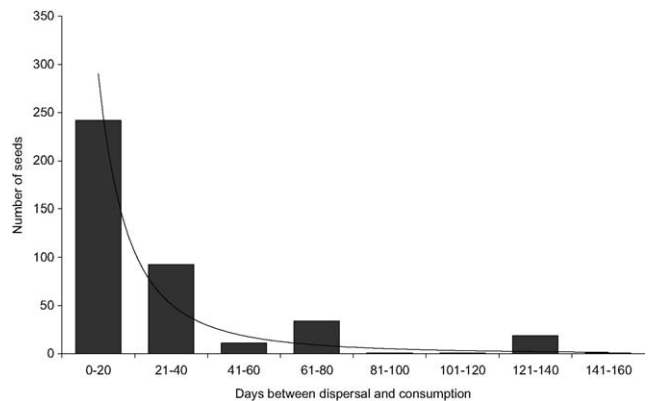


Fig. 2. Number of days elapsed between dispersal and predation (appearance in refuse piles) in the marked-seed experiment. Line represents potential tendency.

Marked seeds moved from the source plant an average distance of 2.50 ± 3.24 m (range 0.30–18.00, $n = 178$ randomly sampled measurements).

On the other hand, 186 and 84 seedlings were found in 1997 and 1998, respectively. Thus, only a very reduced fraction of seeds became seedlings (0.68% and 0.55% of total seed production, respectively). No seeds were found in the soil samples, suggesting the lack of a permanent soil seed bank. Ant seed predation, seedling emergence and seed bank holdings accounted for less than 50% of total seed production. The fate of the remaining seeds is unknown.

E. paularense mericarps found at *M. capitatus* nests weighed 28.37 g in 1997 and 11.91 g in 1998. This represented 3.35% and 2.67% of total refuse piles in 1997 and 1998, respectively (Fig. 3).

3.3. Seed perspective modelling

The binomial GLM model for the probability of a seed escaping from predation that included all variables was highly significant ($\chi^2 = 102.16$, d.f. = 10, $P < 0.001$). The reduced model (Forward Wald stepwise selection) only selected three

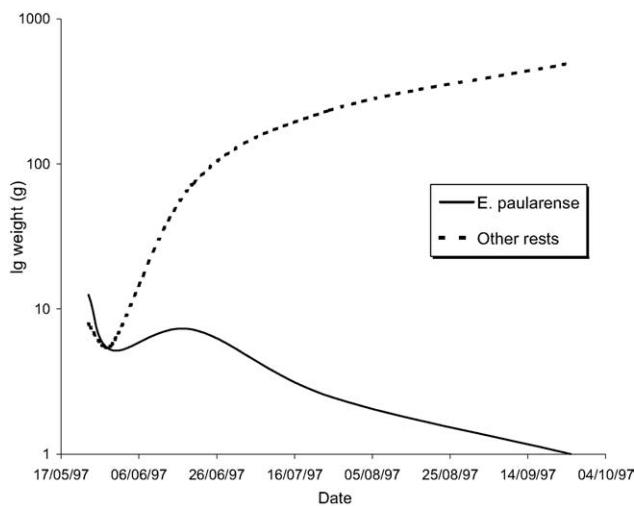


Fig. 3. Weight of *E. paularense* fruit coats in relation to the weight of other species' fruit remains in the refuse piles of *M. capitatus* nests throughout the dispersal period.

of the 11 variables considered in the saturated model. These variables were dummies corresponding to the last three dispersal events (24, 27 and 30-May-1997). Positive coefficients were obtained for the three variables (Table 2). This reduced model was also highly significant ($\chi^2 = 93.10$, d.f. = 2, $P < 0.001$). Comparison of the two nested models (reduced versus saturated) showed that the reduced model was a good substitute for the saturated model ($\chi^2 = 9.06$, d.f. = 7, $P < 0.248$). A complete set of reduced models was also tested and compared by changes in the deviance but none of them improved the final reduced model.

3.4. Plant perspective modelling

The model for the number of seeds per plant escaping from ant predation (log transformed) was highly significant ($r^2 = 0.714$, $F = 49.9$, $P < 0.001$) when the four predictor variables were simultaneously included. Forward selection based on the magnitude of the Cp statistic at each step only selected two variables, total seed production per plant and dispersal time, and provided a highly significant reduced model ($r^2 = 0.712$, $F = 101.33$, $P < 0.001$). Coefficients of both variables in the reduced model were positive and significantly different from 0. Comparison of the two models showed that the reduced model was a good substitute for the saturated model ($\chi^2 = 0.14$, d.f. = 2, $P < 0.936$). A simpler model including only total seed production, which was the first selected variable, was also a good substitute for the model with two predictor variables ($\chi^2 = 0.14$, d.f. = 1, $P < 0.293$).

Table 2

Forward Wald selected variables for the probability of a seed escaping from ant predation. Data from 1997

Selected variables	Coefficients \pm 1 S.E.	Wald statistic	P value
Dispersal date T6	1.38 \pm 0.21	42.02	<0.0001
Dispersal date T7	1.70 \pm 0.27	37.40	<0.0001
Dispersal date T8	1.40 \pm 0.38	13.36	<0.0001

T6 = 24-May, T7 = 27-May, T8 = 30-May-1997.

The coefficient of the predictor in this last model was positive and significantly different from 0 (0.0723 ± 0.005 , $t = 13.81$, $P < 0.001$).

The model for the percentage of seeds per plant escaping from ant predation with the four predictor variables was not significant ($r^2 = 0.082$, $F = 1.79$, $P < 0.138$). A reduced model including only dispersal time (coefficient 0.045 ± 0.020 , $t = 2.272$, $P = 0.026$) was significant at $P < 0.05$ ($r^2 = 0.059$, $F = 5.160$, $P < 0.026$). This last model was a good substitute for the saturated model ($\chi^2 = 0.178$, d.f. = 3, $P < 0.98$).

Number of non-predated seeds and plant size were positively correlated (Spearman $r = 0.243$, $P = 0.025$, $n = 85$). Number of non-predated seeds was also correlated with duration of dispersal period (Spearman $r = 0.625$, $P < 0.001$, $n = 85$).

4. Discussion

4.1. Seed predation

Observations indicate that *M. capitatus* only harvested mericarps with fully-developed seeds and rejected those with aborted seeds or with no seeds. The comparison between the weight of mericarp coats and the weight of fruit remains of other species on the refuse piles, as an estimate of foraging activity, suggests that the fraction of *E. paularense* mericarps was only important at the early stage of the ant foraging period (Fig. 3). Seed predation by ants was estimated to be 27.8% and 17.6%, in 1997 and 1998, respectively. However, more accurate estimations from our experiments with marked mericarps indicate that predation actually reached significantly higher values (43.4% in 1997).

Since the time lag between dispersed seeds and deposition of mericarp coats in the refuse piles is lower than 2 months in most cases, both approaches used to estimate seed predation are valid, although somewhat conservative. The method that counts all mericarp coats in all the refuse piles of the population is sound because it covers the whole population. However, the estimation of seed production introduces further uncertainty in the estimation. The use of marked seeds for estimating seed predation provides a better controlled approach. However, this approach only used data of a sample of the population.

The higher estimates for seed predation in 1997 might be linked to the fact that in this year total seed production almost doubled that of 1998. This would suggest that the relative interest of *M. capitatus* towards *E. paularense* seeds with respect to other food sources may depend on existing availability (Gordon, 1993). Similar results have been found in other ant-species of this genus: *Messor andrei* appears to harvest on preferred species until these seeds are rare (Hobbs, 1985; Brown and Human, 1997).

Under some circumstances seed removal by ants can lead to secondary seed dispersal mechanism after accidental abandonment (Hughes, 1991; Dean and Yeaton, 1992). This is

especially true in the case of plants that produce fruits with many seeds. Thus, when fruit coats are deposited in the refuse piles, they may accidentally contain one or more seeds. *E. paularense* mericarps can only contain one seed. The very small number of unopened mericarps found in the refuse piles in 1997 and their absence in 1998, indicate that almost all seeds transported to the nests were consumed or rarely stored for later consumption. Furthermore, direct observation of ant transport behaviour from harvested plants to their nests led us to reject the possibility of dyszoochory (Wolff and Debussche, 1999), as it has been reported in other *Messor* species transporting morphologically similar diaspores (Schöning et al., 2004).

Emergence in autumn immediately after dispersal, the lack of seeds in soil samples and an almost 100% germination percentage under laboratory conditions (Pérez-García et al., 1995), clearly suggest the absence of a permanent soil seed bank in *E. paularense*. Under such circumstances, seed predation by ants can notably reduce the number of available seeds for germination and the establishment of new individuals.

There is no detailed information on other sources of seed predation that might be at least partly responsible for the substantial percentage of seeds with an unknown fate. We suspect that small mammals whose tracks have been observed in the population, may be implicated (Hoffmann et al., 1995; Gutiérrez et al., 1997). Seedlings that died in the first few days after emergence, which were missed by our autumn seedling surveys, would also contribute to the percentage of seeds with an unknown fate.

4.2. Escaping from ant predation: seed perspective

Seeds dispersed at the end of the dispersal period had the best chances of escaping from ant seed predation. Time pattern in predation (see Fig. 1) suggests that dispersal at the beginning of the period might also be advantageous (positive coefficient in the global model). However, this was rejected in the reduced model possibly due to the low number of seeds dispersed at that moment. Anyway, ants did not select seeds following a density-dependence strategy at this scale (Kunin, 1994) as shown by the rejection of the variables total seed production by each mother plant and total seed production in the neighbourhood in the final model. Rather than taking advantage of high densities of *E. paularense* seeds, it seems that ants only responded to food resources available at each moment in the whole community. At the end of the *E. paularense* dispersal period there is a highly diverse offer of seeds dispersed from other plants in the community (M.J. Albert, J.M. Iriondo and A. Escudero, personal observation). As suggested from the study of the weight of nest refuse piles (Fig. 3), food availability for *M. capitatus* depends on *E. paularense* at the beginning of foraging activity, but this dependence gradually decreases as the season progresses, suggesting a non-specific foraging behaviour. According to Gordon (1993), seeds collected by ants are an expression of preferences and availability with both factors interacting.

As predicted by our model, the unspecific behaviour of ants in their search for food might allow some seeds to escape from predation when other plants in the community disperse their seeds. Synchronisation of dispersal with the rest of the community seems to be an efficient trait to guarantee the escape of a higher number of seeds. Thus, a delay in the time of dispersal would probably provide a higher number of non-predated seeds, and consequently could have important demographic implications.

4.3. Escaping from ant predation: plant perspective

From a whole plant perspective, delayed dispersal time minimised seed predation, thereby maximising the number of escaping seeds both in absolute and relative terms (number and percentage of non-predated seeds, respectively). The positive correlation found between duration of dispersal period and number of non-predated seeds supports the hypothesis that an extended dispersal period favours plant success as it allows a plant to minimise losses from seed predation. Thus, within-individual asynchronous dispersal becomes a favourable trait for minimising seed predation.

Moreover, the model suggested that producing more seeds would be a good strategy for a plant to counteract seed predation pressure. The corresponding Spearman correlation also showed that larger plants, which produced more seeds (Albert et al., 2001a), had a greater number of non-predated seeds.

4.4. Balance between flowering and dispersal phenology

It is widely accepted that adequate timing of flowering and fruiting benefits plant fitness by favouring pollination and seed dispersal (Fenner, 1985; Rathcke and Lacey, 1985; Oberrath and Böhning-Gaese, 2002). Thus, high flowering synchrony within a population increases a plant's ability to attract pollinators when pollinator availability is limited (Faegri and Van der Pijl, 1966). It has also been shown that ant-dispersed plants are in some cases phenologically adapted to their seed dispersers (Turnbull and Culver, 1983; Oberrath and Böhning-Gaese, 2002).

In *E. paularense*, we observed the relevance of flowering synchrony on successful pollination (Albert et al., 2001a). Peak seed dispersal does not coincide with the period of peak activity of *M. capitatus*, suggesting an additional adaptation to avoid seed predation. However, our models show that seed predation in *E. paularense* was lower at the end of the dispersal period, when ant activity was at its highest. As flowering and fruiting in *E. paularense* take place earlier than in most other plants in the community, *E. paularense* seeds were predated until other plant species began to disperse their seeds (see Figs. 1 and 3). Thus, despite the coincidence with the peak activity of *M. capitatus*, *E. paularense* plants with late dispersal escaped from seed predation more successfully than plants with early dispersal.

Since ant seed predation intensity on *E. paularense* greatly depends on the temporal seed dispersal patterns of the whole

plant community, our results suggest that the timing and population synchrony of flowering and fruiting of *E. paularense* plants have not been significantly affected by seed predation mediated selection pressures.

In theory, *E. paularense* plants are also confronted with weighing the benefits of increasing flowering intensity to attract pollinators, against the benefits of increasing flowering duration to reduce seed predation. Albert et al. (2001a) showed that flower intensity did not affect fruit set in *E. paularense* suggesting that the populations were not significantly affected by pollinator limitation. However, in the present work, the positive correlation between duration of dispersal and number of non-predated seeds showed benefits in increasing flowering duration. Further studies are needed to explain the combined effect of pollination and seed predation on flowering and fruiting duration in *E. paularense*.

4.5. Implications for species conservation

Population recruitment after dispersal is limited by post-dispersal seed predation, availability of safe-sites, and factors affecting seedling survival (Harper, 1977; Fenner, 1985; Andersen, 1989). Such interacting factors will determine the number of viable seeds to be incorporated into the population and their location. Current levels of seed predation by ants observed in *E. paularense* populations decrease the number of available seeds for germination and establishment of new plants by nearly 40%. However, the effect of harvester ants on perennial plant populations is not well understood, contrary to their impact on the abundance and distribution of annual and ephemeral plants (Beattie and Hughes, 2002). High predation levels and low recruitment may have not the same implications for a short-living plant as for a long-living chamaephyte such as *E. paularense*.

The availability of safe-sites often seems to be a major factor limiting recruitment in stable populations of long-lived perennials (Andersen, 1989; Yates et al., 1995). *E. paularense* requires crevices on rocky surfaces or shallow soils for germination and establishment but such microhabitats are very scarce. In some populations, carrying capacity may be lower than the number of individuals that would be established if all potentially available seeds germinated, as derived from population viability analyses of this species (Albert et al., 2004). Therefore, seed predation effects in naturally rare populations must be considered in relation to other factors, such as the availability of safe-sites.

Another factor that should be taken into account is that *E. paularense* seeds account for a small fraction of the food obtained by *M. capitatus* each season. Thus, *M. capitatus* may be imposing parallel pressure on other members of the plant community that are relevant competitors of *E. paularense*. Further research in the study of the effect of ant seed predation on endangered plants should focus on the whole plant community if one wished to model the effects of abundance of granivorous ants on the population dynamics of threatened species.

Conservation actions operate in complex systems and must consider all factors that condition target population dynamics. Thus, seed predation by ants is just one factor among many others that affect vital rates. In contrast with results from desert systems (Brown et al., 1979; Davidson et al., 1985), seed harvesting by ants may have not a significant effect on this plant community, although ants harvest large numbers of seeds (Brown and Human, 1997).

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References

- Albert, M.J., Escudero, A., Iriondo, J.M., 2001a. Female reproductive success of narrow endemic *Erodium paularense* in contrasting microhabitats. *Ecology* 82, 1734–1747.
- Albert, M.J., Escudero, A., Iriondo, J.M., 2001b. Environmental range of narrow endemic *Erodium paularense* Fern. Gonz. and Izco and its vulnerability to changing climatic conditions. *Bocconea* 13, 549–556.
- Albert, M.J., Iriondo, J.M., Escudero, A., 2003. *Erodium paularense* Fern. Gonz. and Izco. In: Bañares, A., Blanca, G., Güemes, J., Moreno, J.C., Ortiz, S. (Eds.), Atlas y Libro Rojo de la Flora Vasculare Amenazada de España. Dirección General de Conservación de la Naturaleza, Madrid, pp. 690–691.
- Albert, M.J., Draper, D., Iriondo, J.M., 2004. *Erodium paularense* in Spain: relevance of microhabitats in population dynamics. In: Akçakaya, R.H., Burgman, M.A., Kindvall, O., Wood, C.C., Sjögren-Gulve, P., Hatfield, J.S., McCarthy, M.A. (Eds.), Species Conservation and Management: Case Studies. Oxford University Press, Inc, New York, pp. 75–89.
- Andersen, A.N., 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia* 81, 310–315.
- Beattie, A.J., Hughes, L., 2002. Ant–plant interactions. In: Herrera, C.M., Pellmyr, O. (Eds.), Plant–Animal Interactions. An Evolutionary Approach, Blackwell Science Ltd, UK, pp. 211–235.
- Brown, J.H., Reichman, O.H., Davidson, D.W., 1979. Granivory in desert ecosystems. *Annu. Rev. Ecol. Evol. S.* 10, 201–227.
- Brown, M.J.F., Human, K.G., 1997. Effects of harvester ants on plant species distribution and abundance in a serpentine grassland. *Oecologia* 112, 237–243.
- Crawley, M.J., 1992. Seed predators and plant population dynamics. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. CAB International, Oxford, pp. 157–191.
- Crist, T.O., MacMahon, J.A., 1992. Harvester ant foraging and shrub-steppe seeds: interactions of seed resources and seed use. *Ecology* 73, 1768–1779.
- Davidson, D.W., Inouye, R.S., Samson, D.A., 1985. Granivory in the Chihuahuan desert: interactions within and between trophic levels. *Ecology* 65, 1780–1786.
- Dean, W.R.J., Yeaton, R.I., 1992. The importance of harvester ant *Messor capensis* nest-mounds as germination sites in southern Karoo, South Africa. *Afr. J. Ecol.* 30, 335–345.
- De Steven, D., 1983. Reproductive consequences of insect seed predation in *Hamamelis virginiana*. *Ecology* 64, 89–98.

- European Community, 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Brussels.
- Faegri, K., Van der Pijl, L., 1966. The Principles of Pollination Ecology. Pergamon, London, UK.
- Fenner, M., 1985. Seed Ecology. Chapman & Hall, London.
- González-Benito, E., Martín, C., Iriondo, J.M., 1995. Autoecology and conservation of *Erodium paularense* Fdez. Glez. and Izco. Biol. Conserv. 72, 55–60.
- Gorb, E.V., Gorb, S.N., 2000. Effects of seed aggregation on the removal rates of elaiosome-bearing *Chelidonium majus* and *Viola adourata* seeds carried by *Formica polyctena* ants. Ecol. Res. 15, 187–192.
- Gordon, D.H., 1993. The spatial scale of seed collection by harvester ants. Oecologia 95, 479–487.
- Guisan, A., Zimmerman, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.
- Guisan, A., Edwards Jr., T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157, 89–100.
- Gutiérrez, J.R., Meserve, P.L., Herrera, S., Contreras, L.C., Jaksic, F.M., 1997. Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. Oecologia 109, 398–406.
- Harper, J.L., 1977. Population Biology of Plants. Academic Press, London.
- Harper, J.L., Lovell, P.H., Moore, K.G., 1970. The shapes and sizes of seeds. Annu. Rev. Ecol. Evol. S. 1, 327–356.
- Heske, E.J., Brown, J.H., Buo, Q., 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. Oecologia 95, 520–524.
- Hobbs, R.J., 1985. Harvester ant foraging and plant species distribution in annual grassland. Oecologia 67, 519–523.
- Hoffmann, L.A., Redente, E.F., McEwen, L.C., 1995. Effects of selective seed predation by rodents on shortgrass establishment. Ecol. Appl. 5, 200–208.
- Howe, H.F., Brown, J.S., 2000. Early effects of rodent granivory on experimental forb communities. Ecol. Appl. 10, 917–924.
- Howe, H.F., Brown, J.S., 2001. The ghost of granivory past. Ecol. Lett. 4, 371–378.
- Hughes, L., 1991. The relocation of ant nest entrances: potential consequences for ant-dispersed seeds. Aust. J. Ecol. 16, 207–214.
- Hughes, L., Westoby, M., 1990. Removal rates of seeds adapted for dispersal by ants. Ecology 71, 138–148.
- Hulme, P.E., 1997. Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. Oecologia 111, 91–98.
- Hulme, P.E., 1998. Post-dispersal seed predation: consequences for plant demography and evolution. Persp. Plant Ecol. Evol. S. 1, 32–46.
- Hulme, P.E., Benkman, C.W., 2002. Granivory. In: Herrera, C.M., Pellmyr, O. (Eds.), Plant–Animal Interactions. An Evolutionary Approach, Blackwell Science Ltd, UK, pp. 132–154.
- IUCN, 2001. IUCN Red List Categories: Version 3.1. Prepared by the IUCN Species Survival Commission, IUCN, Gland, Switzerland and Cambridge, UK.
- Janzen, D.H., 1971. Seed predation by animals. Annu. Rev. Ecol. Evol. S. 2, 465–492.
- Kunin, W.E., 1994. Density-dependent foraging in the harvester ant *Messor ebeninus*: two experiments. Oecologia 98, 328–335.
- Louda, S.M., 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. Ecol. Monogr. 52, 25–41.
- MacMahon, J.A., James, A., Mull, J.F., Crist, T.O., 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. Annu. Rev. Ecol. S. 31, 265–291.
- MathSoft, 1999. S-PLUS 2000 Guide to Statistics, volume 1. Data Analysis Products Division. MathSoft, Seattle, Washington, USA.
- McCullagh, P., Nelder, J.A., 1999. Generalized Linear Models (second edition) Monographs on Statistics and Applied Probability 37. Chapman & Hall/CRC, USA.
- Moore, L.R., 1978. Seed predation in the legume *Crotalaria*. I. Intensity and variability of seed predation in native and introduced populations of *C. pallida* Ait. Oecologia 34, 185–202.
- Morton, S.R., 1985. Granivory in arid regions: comparison of Australia with North and South America. Ecology 66, 1859–1866.
- Nicholls, A.O., 1989. How to make biological survey go further with generalized linear model. Biol. Conserv. 50, 51–75.
- Oberrath, R., Böhning-Gaese, K., 2002. Phenological adaptation of ant-dispersed plants to seasonal variation in ant activity. Ecology 83, 1412–1420.
- Pérez-García, F., Iriondo, J.M., González-Benito, M.E., Carnés, L.F., Tapia, J., Prieto, C., Plaza, R., Pérez, C., 1995. Germination studies in endemic plant species of the Iberian Peninsula. Isr. J. Plant Sci. 43, 239–247.
- Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. Annu. Rev. Ecol. Evol. S. 16, 179–214.
- Reichman, O.J., 1979. Desert granivore foraging and its impact on seed densities and distributions. Ecology 60, 1085–1092.
- Roach, D.A., Wulff, R.D., 1987. Maternal effects in plants. Annu. Rev. Ecol. Evol. S. 18, 209–235.
- Schöning, C., Espadaler, X., Hensen, I., Roces, F., 2004. Seed predation of the tussock-grass *Stipa tenacissima* L. by ants (*Messor* spp.) in south-eastern Spain: the adaptive value of trypanocarp. J. Arid Environ. 56, 43–61.
- Spector, P., 1994. An Introduction to S and S-PLUS. Duxbury Press, Belmont, C.A.
- Traniello, J.F.A., 1989. Foraging strategies of ants. Annu. Rev. Entomol. 34, 191–210.
- Turnbull, C.L., Culver, D.C., 1983. The timing of seed dispersal in *Viola nuttalli*: attraction of dispersers and avoidance of predators. Oecologia 59, 360–365.
- Wolff, A., Debussche, M., 1999. Ants as seed dispersers in a Mediterranean old-field succession. Oikos 84, 443–452.
- Yates, C.J., Taplin, R., Hobbs, R.J., Bell, R.W., 1995. Factors limiting the recruitment of *Eucalyptus salmonophloia* in remnant woodlands. II. Post-dispersal seed predation and soil seed reserves. Aust. J. Bot. 43, 145–155.