

Early effects of rodent post-dispersal seed predation on the outcome of the plant–seed disperser interaction

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We analysed two potential effects of post-dispersal seed predation on recruitment of the wild olive tree (*Olea europaea* var. *sylvestris*), a Mediterranean bird-dispersed tree: (a) the limitation of abundance and distribution of seedlings after dispersal, and (b) the selection of certain seed characteristics of the recruited plants. An observational approach was used to compare seed rain among microhabitats, and how it was affected by seed predation. The relation of microhabitat, scrub density, and seed size with predation risk was explored by a field experiment. Seed density ranged from 0 seeds/m² in open places to 93.2 seeds/m² under *O. europaea*. The overall predation rate was low, as shown in the observational approach (35%). The mean percentage of predation in the experimental approach was 51%, ranging across microhabitats between 28% and 88%. It was higher in dense scrub patches (67%) than in sparse ones (33%), and lower for large seeds (42%) than for medium and small ones (57% and 55%, respectively). Finally, seed density near seed depots did not increase their probability of being detected by rodents or the predation rate. Although predation rates were low, wild olive seeds could be frequently found by rodents due to their spatial ubiquity and local abundance. Together with the efficient foraging strategy of predators (92% of experimental seed depots were found), this allowed a widespread post-dispersal predation, but it did not modify the relative distribution of seeds among microhabitats. Thus, in our study, the seed dispersal pattern of the wild olive tree was not reshaped by post-dispersal predation, because (1) rodents did not alter significantly its initial spatial distribution and (2) mice did not seem to limit the number of recruits. Finally, our results indicate that, as a consequence of seed size preferences of rodents, large seeds have a higher probability to survive post-dispersal predation. Thus, seed size may be a key trait to determine the identity of the future recruits in the wild olive tree, at least affecting the characteristics of the seeds that reach the soil seed bank.

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The importance of seed dispersers on individual plant fitness and plant demography is implicit in most of the literature about plant-disperser interactions (Estrada and Fleming 1986, Jordano 1992, Willson 1992, Fleming and Estrada 1993, Herrera 1995). However, the conclusions in these directions arising from studies of fruit removal and seed dispersal are clearly limited since post-dispersal events, seed predation among them, can

be strong selective processes acting immediately after seed dispersal (Schupp 1995, Schupp and Fuentes 1995).

The influence of post-dispersal seed predation on plant recruitment and demography has been hypothesised to be two-folded. At a populational level, it may limit the number and spatial distribution of recruited plants, whereas at an individual level it may determine

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the identity (key characteristics) of the recruits (Andersen 1989, Louda 1995, Hulme 1998). However, as far as we know, no study has simultaneously addressed both effects.

Rodents are among the most important post-dispersal seed predators world wide (Crawley 1992). Many factors may affect their foraging activity; among the most frequently considered are the accumulation of litter on the ground (Price and Jenkins 1986, Schupp 1988a, Myster and Pickett 1993), the cover of different plant species (Herrera 1984, Herrera et al. 1994, Hulme 1997), vegetation structure (Schupp 1988b, Kollmann 1995), the density of seeds (Willson and Whelan 1990, Gryj and Domínguez 1996), and the distance to the mother plants (Howe et al. 1985, Notman et al. 1996). The extent to which these foraging cues match the spatial distribution of dispersed seeds will determine the impact of rodents on both plant population dynamics (by limiting the number of potential recruits) and the spatial pattern of recruitment (by limiting the sites suitable for recruitment).

The relationship between seed traits (mainly seed size) and predation risk has been also frequently addressed (M'Closkey 1980, Kelrick et al. 1986, Hulme 1993, Osunkoya 1994, Blate et al. 1998, Kollmann et al. 1998). However, the knowledge about the influence of the size of seeds on their probability to recruit into a successive stage of the life cycle is very limited, as most research on this topic has been approached through inter-specific comparisons, where many other effects besides size itself can affect the results. A clear assessment of the effect of size on seed fitness can only be approached through intra-specific comparisons.

This paper analyses early effects of rodents on the outcome of the plant–seed dispersers interaction in the wild olive tree (*Olea europaea* var. *sylvestris*). Specifically we address the following questions: (1) How spatially variable is post-dispersal seed predation and to what extent does the variability depend on habitat structure and seed density? (2) Can the identity of the recruited individuals be related to their size through different risk of predation? and (3) Do rodents modify the spatial distribution of seeds generated by avian seed dispersers?

Table 1. Summary table of mean seed characteristics (± 1 SE). Seeds were classified according to three weight classes (as shown below), each apt to be dispersed by a different array of avian frugivores (see Rey et al. 1997).

	Seed size classes			All groups
	Small (<0.1 g)	Medium (0.1–0.2 g)	Large (>0.2 g)	
Seed weight	0.07 \pm 0.003	0.15 \pm 0.003	0.26 \pm 0.004	0.20 \pm 0.005
Seed length	7.37 \pm 0.14	9.39 \pm 0.10	11.6 \pm 0.13	10.3 \pm 0.12
Seed width	4.40 \pm 0.08	5.62 \pm 0.02	6.69 \pm 0.04	6.00 \pm 0.06
Thickness of endocarp	0.96 \pm 0.02	1.04 \pm 0.02	1.27 \pm 0.02	1.15 \pm 0.02
Weight of embryo plus endosperm	0.01 \pm 0.001	0.03 \pm 0.001	0.05 \pm 0.001	0.04 \pm 0.001
Seed dispersers	<i>Erithacus rubecula</i> <i>Sylvia atricapilla</i> <i>Sylvia melanocephala</i> <i>Turdus philomelos</i>	<i>Sylvia atricapilla</i> <i>Turdus philomelos</i>	<i>Turdus philomelos</i>	

Materials and methods

Study species and sites

The wild olive tree is a small tree that occurs along the northern Mediterranean basin. Wild olive fruits ripen throughout the autumn and winter, and contain a single seed (embryo-cum-endosperm) wrapped in a hard endocarp. Hereafter we will use the general term “seed” to refer the whole propagule (embryo plus endosperm plus endocarp). The main parameters of the seeds are summarised in Table 1. Small- to medium-sized frugivorous birds, mainly species of the genera *Turdus* and *Sylvia*, are the commonest seed dispersers of wild olive in southern Spain; larger frugivores, like *Corvus monedula* and *Pyrhrocorax pyrrhrocorax*, only occasionally disperse wild olive seeds in the study area. More details on the plant natural history can be found in Jordano (1987) and Alcántara et al. (1997a, b).

The study was conducted at Sierra Sur de Jaén (37°40'N, 3°45'W; Jaén province, southern Spain), in an area of dense scrubland dominated by wild olive trees (17 trees/ha), *Quercus coccifera* (Fagaceae), *Pistacia terebinthus* (Anacardiaceae), and *Phillyrea latifolia* (Oleaceae) (plant nomenclature follows Valdés et al. 1987). Large scrub patches are scattered throughout the area, among olive orchards, pine forests and old fields used for livestock. This is a common landscape in the transition from lowlands to mountains along the Guadalquivir Valley.

Seed rain and postdispersal predation

From October 1996 to October 1997 we followed the natural pattern of seed rain and predation. To determine the spatial distribution of the seed rain originated by dispersers, we haphazardly placed 10 seed-fall traps (26 cm \times 33 cm \times 5 cm aluminium pans protected with wire mesh to avoid seed removal by rodents) in each of the five most abundant microhabitats throughout the study site. These microhabitats were characterised by the locally dominant woody species: wild olive tree, *P. latifolia*, *P. terebinthus*, *Q. coccifera* and open areas.

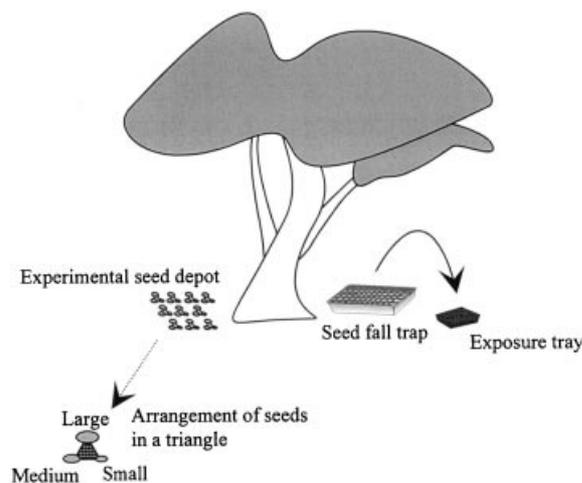


Fig. 1. Design of the sampling stations with the paired observational and experimental arrangements. The observational array (right side of the figure) was composed by a seed-trap and an adjacent tray where trapped seeds were exposed to predators. The experimental array (left side of the figure) consisted of a seed depot with ten triplets of seeds (one of each size).

Traps were monitored fortnightly; all seeds collected by a trap on each review were moved to an adjacent tray (15 cm × 15 cm × 3 cm) of plastic net open to predators (Fig. 1), which was previously monitored to count the number of seeds remaining from the previous review. Litter fallen in the trays was not removed when monitoring so that seeds became naturally hidden during the study period. This method allows the estimation of the number of seeds falling in each sampling point as well as the amount of seeds predated; thus, we can study the temporal dynamics of predation and its effect of reshaping the seed rain.

Experimental analysis

From February 1997 to October 1997 we experimentally tested the effect of seed size and microhabitat type on seed predation. We considered three size classes (see Table 1) matching approximately the sizes dispersed by three different sets of frugivores in the study area (Rey et al. 1997). To test the influence of microhabitat on seed predation we distributed ten experimental depots (replicates) in each of the five microhabitats described above. Every depot was placed adjacent to the sampling points used to study the natural pattern of seed rain and predation (Fig. 1). This paired design allowed to control for effects of seed density nearby the experimental depot. Each depot was composed of ten 3-cm (side) triangles made of plastic mesh nailed to the ground. Each triangle was arranged with one seed of each size glued to the vertexes with a low odour glue (Loctite Durabond 100 NS; Loctite Corp., USA) (see

Herrera et al. 1994 for a similar method). Depots were monitored biweekly. To further analyse the influence of habitat structure on seed predation, in addition to characterising among microhabitats, we also distinguished between points located in two different types of scrub patches within the study site (dense vs sparse patches) depending on the extension and continuity of the scrub canopies. Areas with solitary scrubs, surrounded by several metres of open ground, were considered as sparse patches, while large areas (usually more than 100 m²) composed by intermingled scrub canopies (of the same or different species) were considered as dense patches.

Seeds were solidly glued on the plastic triangles, thus we considered that a seed had been predated if: (1) it was missing from the plastic mesh (which frequently appeared as gnawed); or (2) it was still on the mesh but gnawed. We considered missing seeds equivalent to predated seeds since wood mice (*Apodemus sylvaticus*), the only mouse present in our study area (Rey et al. unpubl.), carries them to deep larder-hoards (Montgomery and Gurnell 1985) from which successful establishment of seedlings is unlikely.

Data analysis

Predation was assessed by estimating seed survival (present vs consumed) at the end of the experiment. We also considered the date of disappearance to explore the timing of predation. Seed survival was examined by logistic analysis (CATMOD procedure used when independent variables were categorical and LOGISTIC procedure with independent continuous variables, SAS Institute 1993). We performed survival analyses to gain a temporal view of the overall predation process. When comparing survival curves between two groups we used Cox-Mantel tests, while Gehan's Wilcoxon tests were applied when more than two groups were analysed. The effect of continuous variables on the survival curve was analysed by a Proportional Hazard-Cox Regression. Finally, variance explained by the effect of scrub patches and microhabitats was obtained with procedure VARCOMP (SAS Institute 1993), using total percentage of predation as dependent variable. Along the text, means are given ± 1 SE unless otherwise stated.

Results

Seed rain

Along the study period, wild olive seeds constituted the bulk of total trapped seeds; other seed species trapped were *Asparagus albus*, *Phillyrea latifolia*, *Rhamnus lycioides* and *Tamus communis*, all of them smaller than wild olive seeds, and accounting together for less than 10% of the seeds accumulated on the trays.

Wild olive seed-fall took place between late October and March. Seed rain was variable among microhabitats (Table 2). All traps under wild olive trees collected seeds, 90% of the traps under *Q. coccifera*, 50% under *P. latifolia* and 40% under *P. terebinthus*; further, there was a significant variation among microhabitats in the number of seeds collected (Kruskal-Wallis test: $H_{(3,n=40)} = 16.7$, $P < 0.001$, open sites excluded). Seed density was highest under wild olive trees, followed by *Q. coccifera*, *P. latifolia*, *P. terebinthus*, and finally open sites. Though no seed was collected in open places in this study, a more extensive research showed that such places did receive a few seeds (3.2 ± 1.0 seeds/m², Alcántara 1998).

General levels of predation – effects on the spatial distribution of seeds

Average estimates of predation rates from the observational approach ($34.6 \pm 7.5\%$) were lower than the ones obtained experimentally ($50.9 \pm 5.6\%$) (Table 2), although the overall levels of predation described by both methods in the sampling stations did not differ statistically (paired *t*-test: $t = 0.6$, $df = 27$, $P = 0.6$). Differences in the number of seeds collected by each seed-trap may seriously affect the estimates of predation rates; thus, analyses based on observational predation estimates may obscure the conclusions about the factors responsible of such predation. We therefore used experimental data to analyse factors influencing the spatial distribution of predation and seed survival.

Our observational approach was mainly designed to explore if predation could modify the spatial distribution of dispersed seeds. It revealed that the amount of seeds predated per sampling point was positively correlated with the amount of seeds fallen at this point ($r_s = 0.65$, $P < 0.001$). However, predation did not overcome the differences in seed density produced by dispersal, as the latter was still strongly correlated with seed density at the end of the study period ($r_s = 0.70$, $P < 0.001$, $n = 28$); furthermore, at this time, differences in seed density among microhabitats were still significant (Kruskal-Wallis: $H_{(3,n=40)} = 10.4$, $P < 0.05$, open sites excluded). We conclude that predation did not modify the relative distribution of seeds among microhabitats.

Table 2. Mean percentage of predation in each microhabitat (± 1 SE). Results from observational and experimental approaches are shown. The observational approach did not allow to estimate a percentage of predation at open places because no seed was collected by the traps placed there.

	Seed density/m ²	Observational approach	Experimental approach
Wild olive tree	93.2 \pm 32.1	38.5 \pm 12.9	29.2 \pm 10.4
<i>Phillyrea latifolia</i>	17.5 \pm 5.9	14.3 \pm 8.0	27.7 \pm 10.9
<i>Pistacia terebinthus</i>	5.8 \pm 2.6	25.0 \pm 20.9	53.0 \pm 12.7
<i>Quercus coccifera</i>	37.3 \pm 14.4	52.3 \pm 15.4	87.7 \pm 5.3
Open places	0	no data	57.0 \pm 12.8

Effect of habitat structure and seed size on predation

Seed density next to the experimental depots was not correlated with the predation rate ($r_s = -0.16$; $P = 0.26$, $n = 50$). After nine months of exposure, rodents were able to discover (i.e. predation had occurred) all experimental depots under wild olive trees, *Q. coccifera*, and at open places, while one under *P. terebinthus* (10%) and three under *P. latifolia* (30%) remained undiscovered (or, at least, untouched). The temporal pattern of discovery of seed depots influenced the predation rate, as shown by the negative correlation between the first date in which predation occurred and final predation rate ($r_s = -0.47$, $P < 0.001$, $n = 50$). Thus, the sooner a depot was located, the higher the final predation rate it suffered. We performed a survival analysis to highlight factors influencing the schedule of finding seed depots (Table 3). Time needed by predators to find a depot was similar between microhabitats, but shorter in dense than in sparse patches. This suggests that rodents were able to scan efficiently the whole study site, although seed depots in dense patches were found earlier. Moreover, searching patterns seemed to be independent of seed density as the latter did not influence the timing of the discovery process.

The spatial distribution of points with similar levels of predation approximately fitted the distribution of both types of scrub patches. To examine such fitting as well as the effect of microhabitat and seed size on predation risk we performed a logistic analysis, with survival of each seed (present vs consumed) as the dependent variable ($n = 1485$). Our model only considered the main effects of the three factors mentioned above and the second-order interactions among them (Table 4). The final model fitted the data correctly ($\chi^2_6 = 5.16$, $P = 0.58$). Both overall habitat structure (type of scrub patch, microhabitat, and their interaction) and seed size influenced the probability of seed survival. The interaction between habitat structure and seed size was not significant. Predation was higher in dense patches ($67.1 \pm 7.4\%$ vs $33.4 \pm 6.9\%$), and especially under *Q. coccifera* (Table 2). Regarding size, large seeds were consumed less frequently than medium and small ones (42.4%, 56.8% and 54.9% respectively). The significant interaction between the type of scrub patch

Table 3. Analysis of the temporal patterns of discovery of the experimental seed depots by rodents (date when the first seed disappeared from each depot): effect of seed density nearby each depot and comparison between microhabitats and patch types.

Effect	Test	Results	P
Microhabitat	Gehan's Wilcoxon	$\chi^2_4 = 6.42$	0.17
Type of scrub patch	Cox-Mantel	$Z = -1.82$	0.03
Seed density nearby	Proportional Hazard (Cox) Regression	$\chi^2_4 = 0.00$	0.98

and microhabitat arises because predation under *P. latifolia* was similar in both types of scrub patch, while it was higher in dense ones for all other microhabitats. When examining separately the effect of habitat structure (by two-factor ANOVA), it turned out that type of scrub patch and microhabitat accounted for similar percentages of variance (25.7% and 20.3%, respectively). These two factors and their interaction explained 53.3% of the total variation in predation.

These analyses are referred to the survival probability at the end of the study period; however, it is also interesting to examine how long seeds survived (survival analysis, see Table 5). The size of a seed significantly influenced its mean survival (i.e. larger seeds survived for longer, Fig. 2A). Microhabitat had also a significant effect on survival: seeds under *Q. coccifera* were predated earlier, while those under wild olive trees and *P. latifolia* disappeared, on average, three months later (Fig. 2B). Similarly, seeds placed in sparse scrub patches escaped from predation longer than seeds in dense scrub (Fig. 2C). Finally, predation risk was significantly related to seed density, although the beta coefficient of the regression (close to 1) suggests that it decreased only slightly with increasing density.

Results obtained from the survival and logistic analyses are generally consistent and show that both temporal predation patterns and its final outcome differed among microhabitats, type of scrub patch and seed size.

Discussion

Factors influencing the spatial distribution of predation rates

Wild olive seeds have three potential groups of post-dispersal consumers: 1) At least three ant species have been observed carrying wild olive seeds during the study (*Messor capitatus*, *M. barbarus* and *Aphaenogaster senilis*); however, their incidence can be considered negligible (see also Hulme 1997). 2) The only bird species able to predate on ripe wild olive seeds, the hawfinch (*Coccothraustes coccothraustes*), is scarce in our study area (Alcántara et al. 1997a), and thus its activity as a seed predator can also be discarded. 3) Finally, the only rodent trapped in periodical sampling trials in our study site, over two years, was *A. sylvaticus* (unpubl.); further, all predated seeds found had distinctive rodent teeth marks. Therefore, *A. sylvaticus* ap-

pears to be the almost exclusive post-dispersal seed predator of this plant species in the study area.

Apodemus sylvaticus is highly efficient in searching for seeds as evidenced by the high proportion of sampling points where predation occurred (92%; see also Hansson 1985, Santos and Tellería 1991). However, the overall predation level of wild olive seeds in our study site is relatively low. Moreover, predation varied spatially, both at the microhabitat and patch scales, as shown in other studies (see for example Herrera 1984, Schupp 1988b, Horvitz and Schemske 1994). The observed aggregation of points with a similar predation rate probably reflects the spatial foraging patterns of predators (Willson 1988). Habitat structure seems to determine the habitat preferences of the rodents, due either to food availability (M'Closkey 1983, Angelstam et al. 1987, Simonetti 1989), protection against predators (Kotler et al. 1991, Díaz 1992, Bowers and Dooley 1993), or suitable thermoregulatory conditions (Grodzinski 1985). *Apodemus sylvaticus* usually prefers dense scrub and forest stands, especially in winter (Tellería et al. 1991, Díaz 1992). Accordingly, we found that predation, which began during winter, occurred earlier in the dense scrub patches. This may account for the higher predation found there and in related microhabitats (like *Q. coccifera*), as the date when a seed depot was first predated was positively related to the percentage of predation it finally suffered. Many authors have shown that in temperate areas seed predation is higher in dense scrub than in areas with sparse vegetation (Mittelbach and Gross 1984, Gill and Marks 1991, Bowers and Dooley 1993, Hulme 1994, 1996, 1997, Kollmann 1995; see, however, Bustamante et al.

Table 4. Logistic analysis of the effect of the type of scrub patch, microhabitat and seed size on the probability of seed survival, estimated as the presence/absence of each seed ($n = 1485$) at the end of the experiment.

Effects	χ^2 (dF)	P
Intercept	0.13 (1)	0.72
Type of scrub patch (TSP)	71.1 (1)	<0.001
Microhabitat	82.0 (4)	<0.001
TSP × microhabitat	47.6 (3)	<0.001
Seed size	37.0 (2)	<0.001
TSP × seed size	0.29 (2)	0.86
Microhabitat × seed size	9.54 (8)	0.30
Model adjustment	5.16* (6)	0.58

* Maximum likelihood χ^2 .

Table 5. Experimental approach of seed survival. Survival analyses for the effects of seed size (three categories), microhabitat (five categories), type of scrub patch (two categories) and seed density (continuous variable).

Effect	Class	Mean life (days \pm SD)
Seed size [‡] $\chi^2_2 = 34.0$, $P < 0.001$	Small (<0.1 g)	157.2 \pm 3.5
	Medium (0.1–0.2 g)	158.7 \pm 3.3
	Large (>0.2 g)	181.6 \pm 3.0
Microhabitat [‡] $\chi^2_4 = 307.5$, $P < 0.001$	Wild olive tree	190.8 \pm 4.1
	<i>Q. coccifera</i>	111.4 \pm 3.6
	<i>P. latifolia</i>	204.6 \pm 2.9
	<i>P. terebinthus</i>	155.4 \pm 4.4
	Open places	168.4 \pm 4.1
Type of scrub patch* $Z = -15.38$, $P < 0.001$	Dense	137.6 \pm 2.7
	Sparse	194.6 \pm 2.3
Density $\chi^2_1 = 18.08$, $P < 0.01$ [†]	Coefficient $\beta = 0.997$	

[‡] Gehan's Wilcoxon test.

[†] Proportional Hazard (Cox) Regression. Effect of seed density nearby the sampling point on individual seed survival.

* Cox-Mantel test.

1996). Finally, predators' satiation may account for the low predation rate found under conspecific trees (Janzen 1982), as seed density in this microhabitat was very high. In fact, considering the mean seed density and the mean predation rate in each microhabitat, we estimated that rodents could consume ca 42 seeds/m² under wild olive trees, more than twice the amount than under *Q. coccifera* (16 seeds/m²), and much more than under *P. latifolia* (2.39 seeds/m²) or *P. terebinthus* (1.17 seeds/m²).

These results suggest that *A. sylvaticus* does not search selectively for wild olive seeds, as consumption rates were low and determined by habitat characteristics not related to the density of wild olive seeds itself.

Seed size and the probability to escape from predation

Size is a phenotypic trait that may allow seeds to escape from rodent predation and, thus, to recruit into the next stages of the life cycle. Most studies which focused on seed size selection by rodents agree that larger seeds may suffer a higher predation risk (see for example Kelrick et al. 1986, Podolski and Price 1990, Willson and Whelan 1990, Boman and Casper 1995); however, this is not a rule, as shown by other studies (Tripathi and Khan 1990, Osunkoya 1994, Blate et al. 1998, Kollmann et al. 1998) and by our experimental results. Several authors suggest that seed size-related traits, more than size itself, may affect the ease of manipulation and selection criteria by rodents (Rosenzweig and Sterner 1970, Ebersole and Wilson 1980, Kelrick et al. 1986, Kollmann et al. 1998). For instance, the thickness

of seed covers (hard structures like endocarp or testa) is usually positively correlated with seed size (Lee et al. 1991, Blate et al. 1998), and the thicker the cover the longer the time needed to reach the edible part of the seed (Kaufman and Collier 1981). Wild olive seeds are protected by a very thick endocarp (see data in Blate et al. 1998 for comparison), which probably makes them less profitable for rodents than many other seeds with thinner protection. For example, Hulme (1997) computed a predation rate (mostly by *A. sylvaticus*) of less than 5% for the thick-walled *Crataegus monogyna* seeds, around 60% for *Prunus mahaleb* seeds (intermediate endocarp thickness) and 87% for *Taxus baccata* seeds, which have the thinnest protection. This rationale may explain the preference for smaller wild olive seeds in the present experiment. Larger wild olive seeds have a thicker endocarp (Alcántara 1998) in relation to the amount of embryo-cum-endosperm. As a consequence, larger seeds must be manipulated for longer to reach a proportionally smaller edible tissue, thus being less energetically rewarding than the smaller seeds.

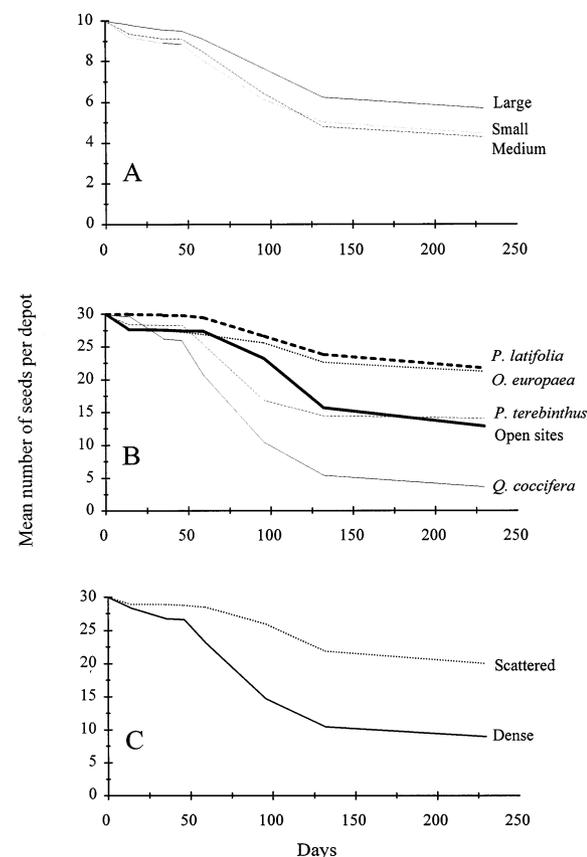


Fig. 2. Temporal pattern of predation for seeds (A) of different size, (B) in different microhabitats, and (C) in different scrub density. For each treatment, lines represent the mean number of seeds surviving averaged across sampling stations. Error bars have been omitted to improve the clarity of the figure.

Seed rain and predation – potential effects on recruitment

The spatial distribution of wild olive seeds in our study site was strongly influenced by the occurrence of different microhabitats, so that four trends could be stated. First, frugivores deposited seeds mainly beneath fruit-bearing wild olive trees. As a result, seed density was, on average, four times higher there than in any other microhabitat. Second, open sites received very few seeds. Third, seed density was also highly variable within microhabitat. Fourth, in spite of the clumped distribution of seeds, seed rain was ubiquitous since more than 56% of the total sampling points received at least one seed. This ubiquity is even higher when we consider only places under scrub cover (70%). Similar percentages have been found for other bird-dispersed seeds like those of *P. latifolia* (Herrera et al. 1994) and *Cornus controversa* (Masaki et al. 1994). In short, from the viewpoint of the postdispersal seed predators, wild olive seeds are a food source frequently found due to its ubiquity, and although its abundance was patchily distributed, it still was spatially predictable.

In our study, seed rain can be considered “resistant” to postdispersal predation as rodents did not alter significantly its initial spatial distribution; a similar result was found by Herrera et al. (1994) for *P. latifolia* in a close geographic area and with the same seed predator (*A. sylvaticus*). On average 17.2 ± 0.03 seeds/m² survived predation. The only microhabitat where predation rate was really high was under *Q. coccifera*; however, the high seed density there allowed an average survival rate of 15 seeds/m². Crop sizes during the study year were intermediate within the supra-annual cycle of fruit production in this species. We therefore would expect a higher number of surviving seeds in years with higher crop sizes. Moreover, the wild olive tree establishes a persistent soil seed bank, sensu Baker (1989). This effect also suggests that post-dispersal seed predators are not able to alter significantly the spatial patterns of recruitment of the wild olive tree (see also Herrera et al. 1994, Hulme 1996). Nonetheless, we cannot conclude that predation did not affect recruitment rate at all, as factors like germination success and seedling survival should also be considered (Schupp 1990, Herrera et al. 1994, Houle 1994, Kollmann 1995). For example, this would be the case if wild olive seedlings required particular nurse plants for establishment, then high rates of seed predation in these microhabitats may still limit rates of colonisation.

Several factors may account for the resistance of wild olive seed rain against rodents: a) its spatial ubiquity that allowed seeds to reach places seldom visited by mice; b) the high seed density in microhabitats frequently surveyed by rodents (for instance, *Q. coccifera* and wild olive tree), with potential satiation effects; and c) the hard seed coat that makes them less profitable than other food types.

Even if predation does not limit recruitment directly, Andersen (1989) warned that it could strongly select the individuals establishing in places suitable for the future of the seedling. Our results support such a view, as rodents clearly selected the size of the seeds consumed. Furthermore, some evidence shows that seed germination and seedling survival in wild olives are positively related to seed size (Alcántara 1998). Thus, seed size may be a key trait to determine the identity of the future recruits in the wild olive tree, as it affects the characteristics of the seeds that are incorporated into the soil seed bank.

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