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Research article

Spatial patterns of seed predation by harvester ants (*Messor* Forel) in Mediterranean grassland and scrubland

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Summary. Seed predation by harvester ants is one of the main processes involved in the seed bank dynamics of Mediterranean grassland and scrubland. We investigated the spatial patterns of seed predation by *Messor* spp. in these systems from a multi-level approach (nest-site selection, foraging patch selection and seed predation risk), using ten experimental plots (20 m × 40 m) set in central Spain. All habitats in grasslands are dominated by *M. barbarus*, while in scrubland this species shares seed exploitation with *M. bouvieri*. In this type of system, the nest-hole and foraging territory distribution of the two species show a certain degree of segregation. *Messor bouvieri* focuses on the exploitation of dry scrub, while *M. barbarus* also forages on subhumid and humid patches. We interpret this as a consequence of the different foraging behaviour and nest site requirements of the two species. In general, the spatial distribution of seed predation risk reflects the patterns detected for the nest-holes and foraging areas, although scrubland has a more heterogeneous predation pattern than grassland.

Key words: Granivory, nest-holes, foraging territories, predation risk, seed harvest.

Introduction

Messor harvester ants are the main seed predators in Mediterranean grasslands (López et al., 1993b; Cerdá and Retana, 1994), and also in certain types of camephyte scrubland (Willott et al., 2000). One of the main features of these communities is the predominance of annual species (Peco, 1989; Fernández Alés et al., 1993; Ortega et al., 1997), which makes their annual regeneration heavily dependent on the soil seed bank dynamics (Peco et al., 1998). Despite its importance, there has been little research into seed predation in these types of systems, particularly in comparison with other aspects such as dispersal (Malo and Suárez, 1995; 1996) or the germination and establishment phases (Espigares and Peco, 1993; Espigares and Peco, 1995).

Patterns of seed predation by *Messor* harvester ants are subordinate to the spatial structure of the ecosystems (Díaz, 1992; López et al., 1993a;1993b; Wilby and Shachak, 2000). In Mediterranean grassland and scrubland a large part of the environmental variability is linked to the gradients generated by the topography and the presence of dispersed tree cover (Bernáldez et al., 1969; González-Bernáldez and Pineda, 1980; Rivas Martínez et al., 1980; De Pablo et al., 1982; Gómez, 1991; González Bernáldez and Peco, 1991). These gradients lead to a mosaic of habitat types differing in microclimate, soil properties, water and nutrient availability, community composition, vegetation structure, productivity and seed availability. These factors can affect patterns of seed predation at least at three levels: nest-site selection, foraging patch selection and foraging intensity.

Nest-site selection by ants is normally related to abiotic factors such as soil properties and degree of solar exposure (Sudd and Franks, 1987; Díaz, 1991; Gordon, 1991; Dean et al., 1997), and also to vegetation structure (Briese, 1982). Nest-holes must be as close as possible to the foraging areas, selected mainly on the basis of seed availability (López et al., 1993a; 1993b; Wilby and Shachack, 2000). Vegetation structure can also affect the accessibility of certain habitats and modify microclimate conditions, on which ant activity is heavily dependent (Cerdá et al., 1988; 1998; Kaspari, 1993). Both nest site and foraging patch selection can be affected by certain biotic interactions, particularly predation on ants (Munger, 1984; Gotelli, 1996) and interference amongst seed-eating ants (Whitford et al.,1976; Brown and Davidson, 1977; Gordon, 1993; Gordon and Kulig, 1996). Finally, foraging intensity is partly determined by the patterns of nest-site and foraging patch selection, but can also vary at a finer scale. The clumped structure inherent to the trunk trail system, as well as local changes in microenvironmental conditions linked to vegetation structure, can lead to a heterogeneous distribution of seed predation risk and hence to the existence of small refuge microsites within the harvester ant foraging areas.

The present study analyses the spatial patterns of seed predation in Mediterranean grassland and scrubland using this multi-level approach. Firstly we ask whether there are differences in *nest-hole density* between *system types* (grassland *vs.* scrubland) and *habitat types*. Secondly, we analyse the effect of these factors on the distribution of the harvester ant *foraging areas*. If there are specific spatial patterns in the nest-hole density and foraging areas, we may expect the *seed predation risk* to also respond to the same spatial factors at a broad scale, the third aspect broached by the study. Finally, we also analyse the spatial distribution of *seed predation risk* at a intra-habitat scale.

Materials and methods

Study area

Fieldwork was conducted in the San Pedro Peak zone (40°38′N, 3°70′E, 35 km north of Madrid, Spain) in 1996 and 1997, in an experimental area covering approximately 2000 ha. on pre-Ordovicic gneiss at an average altitude of 900 m. The somewhat continentalised mediterranean climate has a mean annual temperature of around 13°C and approximately 550 mm annual rainfall, with a severe summer drought and considerable interannual rainfall differences.

The landscape is dominated by two types of clearly differentiated systems – grassland and camephyte scrubland. The grasslands are the product of extensive livestock grazing over the last few centuries, with cattle and some horse grazing at present. There is a high level of species richness (close to 20 species/0.04 m^2; F. M. Azcárate and B. Peco, unpubl. data) predominantly *Poa bulbosa* L. and diverse annuals including *Xolantha guttata* (L.) Raf*., Leontodon taraxacoides* (Vill.) Mérat subsp. *longirrostris* Finch & P. D. Sell*, Hypochoeris glabra* L. and *Trifolium glomeratum* V., which are displaced by perennials such as *Festuca rothmaleri* (Litard) Mark., Dann., *Hypochoeris radicata* L. and *Ranunculus paludosus* Poiret in the moist depressions. Resource availability in grassland increases markedly from dry to moist habitats (92.67 mg/dm^2 and 159.29 mg/dm^2 of ant-collectable seed material respectively; F. M. Azcárate and B. Peco, unpubl. data).

Scrubland areas are located in abandoned grassland and dry farming croplands. They are generally young formations (less than 30 years old), dominated by the pioneer species *Lavandula stoechas* L. subsp. *pedunculata* (Miller) Samp. ex Rozeira, accompanied by other camephytes such as *Halimium umbellatum* (L.) Spach subsp. *viscosum* (Willk.) O. Bolòs and Vigo. Beneath this woody canopy is a thinner herbaceous layer, also rich in annuals, like *Coronilla repanda* (Poiret) Guss. subsp. *dura* (Cav.) Coutinho, *Xolantha guttata*, *Teesdalia coronopifolia* (J. P. Bergeret) Thell. or *Mibora minima* (L.) Desv., and the cryptophyte *Poa bulbosa*. Perennial species, like the tussock-forming grasses *Agrostis castellana* Boiss. et Reut. and *Festuca ampla* Hackel increase their cover in the moister hollows, where the woody species disappear altogether, forming small grassy patches known as *vallicares*, which are also more abundant in seed resources (170.28 mg/dm^2, vs. 84.95 mg/dm^2 in dry scrubland). The term *scrubland* is used throughout the paper in a broad sense, referring to the whole system including the *vallicar* patches. Both grassland and scrubland include scattered trees (40–50 indiv. per ha.), primarily *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. and *Juniperus oxycedrus* L. subsp. *badia* (H. Gay) Debeaux.

Three species of harvester ants have been found in the area. *Messor barbarus* (L.) and *M. bouvieri* (Bond.) are common sympatric species in open environments of the Western Mediterranean and North Africa (Cerdan, 1989). The third species, the less frequent *M. hispanicus* Santschi, has been reported on the Iberian Peninsula, the Balearic Islands (Collingwood, 1976) and in northern Morocco (Cagniant and Espadaler, 1997).

Sampling design

In March, 1996, five 40 m × 20 m plots were set in each type of system (grassland vs. scrubland), with a minimum separation of 200 m and a good representation of the different habitat types resulting from the slope-hollow gradient and the scattered trees. Each plot was characterised at a $1m^2$ scale using 4 habitat types: (1) *humid* or low sectors, with productive soils rich in fine particles and clear signs of accumulation of water for some months of the year; (2) *dry* habitats or slope zones, with a predominance of erosion and little water retention; (3) *subhumid* habitats, used for the transition zones; and (4) *shaded* habitats, for those areas under the tree canopy, typically in dry positions on the slopes. The dry habitats (41.4%) predominated over the subhumid (22.3%), humid (15.1%) and shaded (14.2%) areas. We also distinguished transition areas between the open and shaded habitats, with a few dead leaves and shade for only a few hours a day. However this type of habitat was excluded from all the analysis because of its small area (approx. 6% of the sampled area, less than 1% in some plots).

The following variables were measured in these 10 plots:

1) *Nest-hole distribution*. In August 1996 and 1997, we mapped the nest-hole locations of the 3 *Messor* species (Fig. 1) and estimated a mean value of *nest-hole density* per habitat type. A *Messor* colony may have a large number of entrances with as much as several metres between each one (Cerdan, 1989; López et al., 1993a), making difficult the differentiation of ant colonies. However, for the aim of this study, we did not consider it necessary to individualise colonies, given that seed predation will respond to each active nest-hole.
2) *Foraging areas*. The presence of trunk trails was considered to be an indication of a potential foraging area, regardless of their trophic value. Of the three *Messor* species, only *M. barbarus* constructs conspicuous trunk trails for food searching, collection and transport (Cerdan, 1989; López et al., 1993b; Reyes-López and Fernández-Haeger, 2001), while those of *M. bouvieri* and *M. hispanica* are more seasonal and less visible. We therefore focused on *M. barbarus* in this part of the study. The *M. barbarus* trunk trails were mapped in August 1996 and 1997 in the 5 grassland plots, but only in 1997 in the 5 scrubland plots (Fig. 1). When a worker reaches the end of a trail, it forages in the nearby area. To estimate an index of the area accessible by the workers from the trunk trail network, we divided each plot into 800 1 m^2 quadrats. Each subplot was defined by its habitat type and the presence (0 vs.1) of trunk trails. Finally, we defined the *proportion of subplots crossed by trails* (PST) for each plot and habitat type, and used these values as indicators of the extent of the foraging areas. The physical trunk trails of *M. barbarus* remain visible for several weeks even if they are not used (López et al., 1993b), eliminating the risk of bias due to the difference between the sampling period (August) and the months of maximum seed production in certain habitats (May–June in dry areas).
3) *Seed predation risk*. The ants were offered trap-trays filled with canary seeds (*Phalaris canariensis* L.; approx. 7.05 mg/seed) to obtain a relative standardised estimate of predation risk in function of habitat type. The seeds were left in 3 g lots (approx. 426 seeds) on 9 mm diameter plastic Petri dishes covered by 4 mm steel mesh to protect them from vertebrate predation. Two 1 cm wide entrances were made in every dish to facilitate ant access. The dishes were distributed regularly in 3 plots per system type, forming a rectangular grid with 4 m separations, totalling 50 trays per plot. They were left at midday on 27 August 1997 and then checked every 24 hours for 75 days, with the unconsumed seeds retrieved at the end. Each point was defined by its habitat type and, in the scrubland plots, by the presence/absence of a shrub shading the bait tray. The inverse of the *survival time* (ST) of the dishes, measured as the number of days they remained undiscovered by the ants, was used as an indicator of the predation risk (1/ST+1). *Messor* spp. respond strongly to this type of bait, which was previously tested in the area and has also

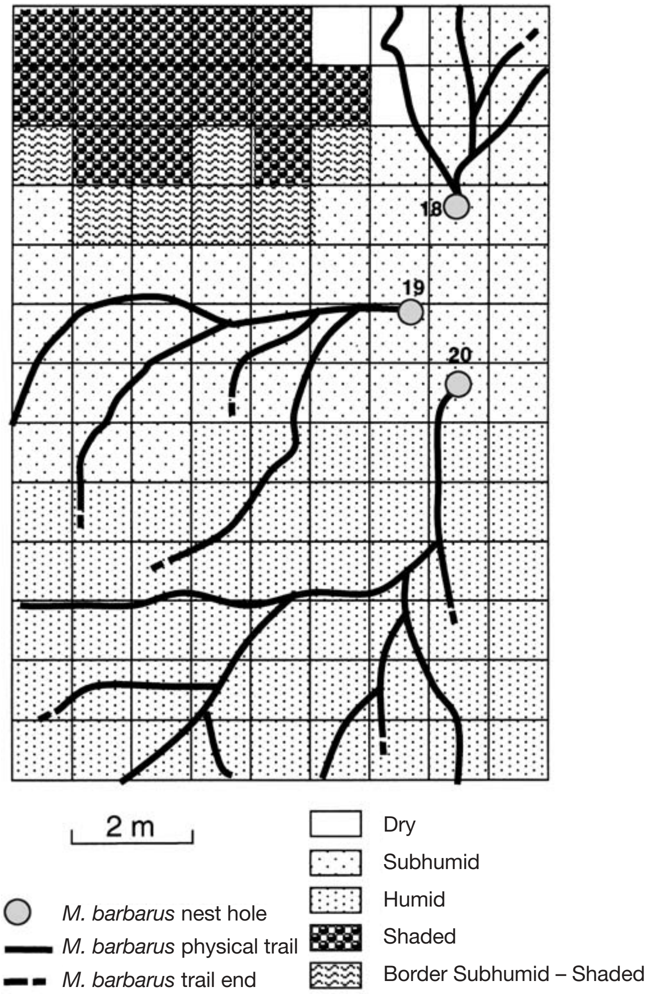

Figure 1. Portion of a grassland plot, showing positions of *Messor barbarus* trunk trails and nest holes in 1996, and the distribution of the habitat types

been used in similar studies (Díaz, 1992). Other species in the area with a broad diet such as *Aphaenogaster iberica* Em. do not show mass recruitment, and thus never empty the trays in less than 24 h. We did not detect any nest-holes of this species alongside the trays. In addition, canary seeds are too heavy to be collected by smaller ants in the area whose strategy does include mass recruitment (e. g., *Pheidole pallidula* Nyl., *Tetramorium hispanica* Em., *Tetramorium semilaeve* André; see Retana et al., 1992 for maximum prey weight of these species).

Statistical analysis

We carried out several ANOVAs to evaluate the effects of the *habitat type* and *system type* on the variables *nest-hole density* (for each *Messor* species), PST (for *Messor barbarus*) and 1/ST, using the plot as the sampling unit. *Habitat type* was included as a repeated measurement factor, while the *system type* (grassland vs. scrubland) was considered as a between-group factor with fixed effects. We were able to test the effect of the *year* on the first two variables as a new repeated measurement factor. Due to the lack of 1996 data on *Messor barbarus* foraging areas in the scrubland plots, in this case we had to carry out planned comparisons with different data subsets to test the effect of each factor, and thus some interactions could not be analysed.

The dry habitat was the only one with enough bait trays to permit a seed predation risk analysis at a more detailed spatial scale. The analysis was applied separately to each of the six plots, and consisted of fitting the variable *survival time* to a Poisson distribution in order to discern whether the variable was randomly distributed, analysing the fit with the Kolmogorov-Smirnov test. We also obtained the quotient between sample variance and mean as an indicator of the sign of the deviations from random. Finally, for each scrubland plot we analysed the effect of woody cover presence on *predation risk* using *t*-tests.

Prior to the parametric tests (t-test, ANOVA and MANOVA), we ensured that the data fit the required assumptions of normality and homoscedasticity (Zar, 1996).

Results

Nest-hole distribution

Messor barbarus nest-hole densities were higher than *M. bouvieri* in both scrubland and grassland (Fig. 2), with almost no nest-holes of the latter species found in grassland. *M. barbarus* only showed significant differences between habitats ($F_{3,24} = 10.43$, $P < 0.001$), while *M. bouvieri* had differences between habitats ($F_{3,12} = 3.51$, $P = 0.049$) and also between years ($F_{1,4} = 8.06$, $P = 0.047$). Both *M. barbarus* and *M. bouvieri* negatively selected moister and shaded habitats to build their colonies, increasing their nest-hole density in subhumid and dry sectors (Fig. 3). *M. bouvieri* nest-holes were more frequent in dry habitats, while those of *M. barbarus* were less restricted to one habitat type, and were also abundant in subhumid areas. The infrequency of *M. hispanica* in the zone (only four nest-holes detected in 1996) impeded statistical analyses using this species.

Messor barbarus *foraging areas*

The extent of *Messor barbarus* foraging areas depends on the habitat type ($F_{3,24} = 27.79$, $P < = 0.001$), with a progressive increase from dry to humid habitats, and a clear rejection of the shaded ones (Fig. 4). The ANOVA did not yield any significant effect of the system type and year.

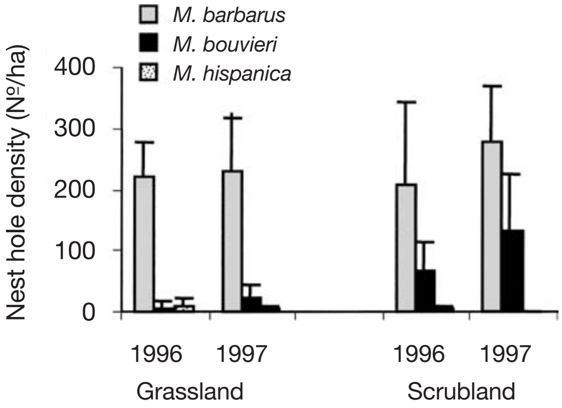

Figure 2. Mean nest-hole density of *Messor barbarus, M. bouvieri* and *M. hispanica* recorded in each system type in 1996 and 1997. N = 5 plots (40 m × 20 m)/system type. Y bars show standard deviations

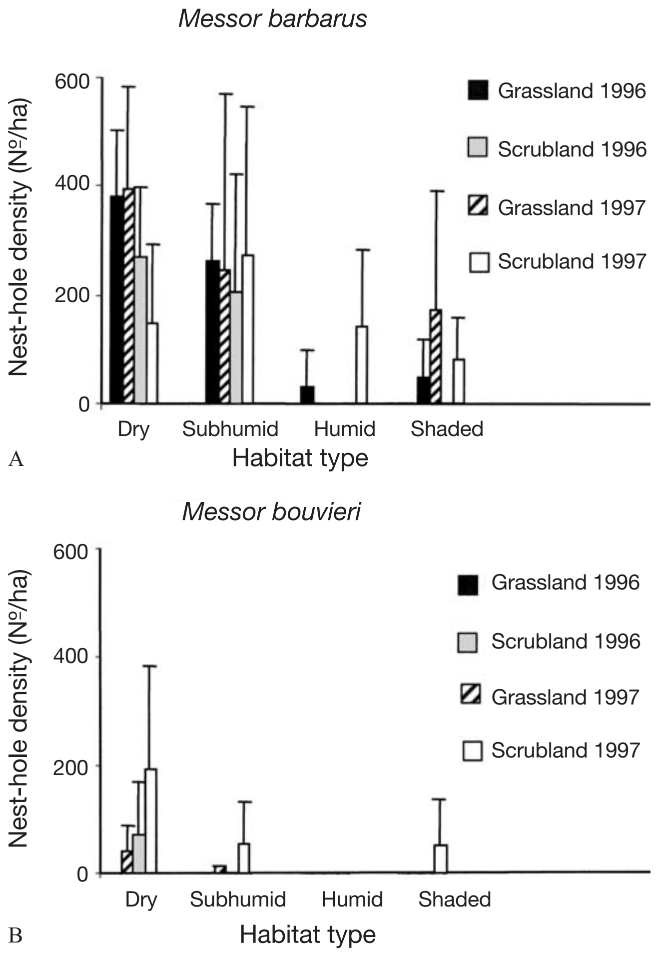

Figure 3. Mean nest-hole density of *Messor barbarus*, A) and *M. bouvieri*, B) for each system and habitat type in 1996 and 1997. N = 5 plots (40 m × 20 m)/system type. Y bars show standard deviations

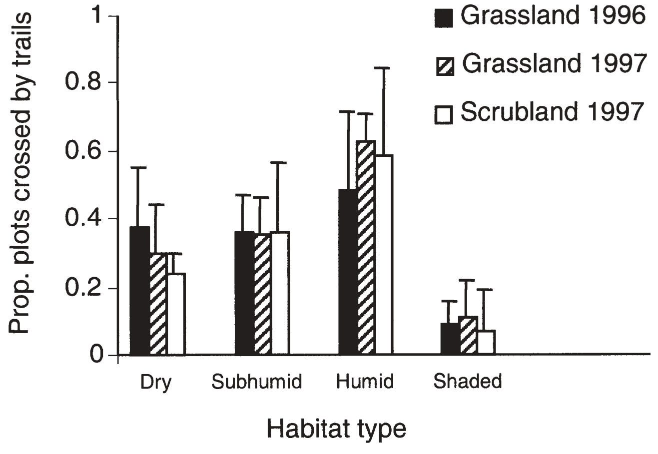

Figure 4. Proportion of 1 m^2 subplots crossed by *Messor barbarus* trails, PST) for each system and habitat type in 1996 and 1997. N = 5 plots (40 m × 20 m)/system type. Y bars show standard deviations

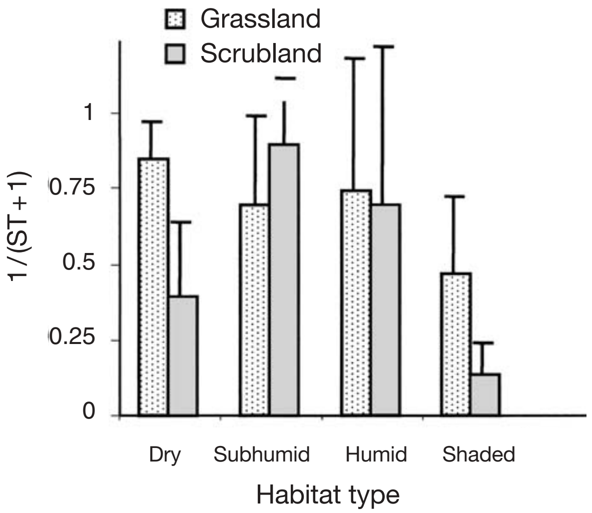

Figure 5. Mean values of the inverse of the *survival time,* 1/ST+1) of seed baits with respect to system and habitat types. N = 3 plots, 40 m × 20 m)/system type. Y bars show standard deviations

Seed predation risk

The *habitat type* was the only factor with significant effects on 1/ST ($F_{3,12} = 4.06$, $P = 0.033$). While the effect seemed to be more obvious in scrubland than grassland (Fig. 5), the analysis did not detect any significant effect for the *system type* x *habitat type* interaction ($F_{3,12} = 1.83$, $P = 0.195$), possibly due to the low power associated with the small sample size ($1\text{-}\beta = 0.248$; critical $F_{3,12} = 3.49$). The figure suggests that in scrubland systems the predation risk is particularly high in subhumid habitats and low in shaded ones; while in grasslands there are no big differences amongst the open areas (dry, subhumid and humid), which show higher values of 1/ST than shaded habitats.

Focusing only on dry habitats, the spatial pattern for the *survival time* of the baits clearly varied between grassland and scrubland. The former tended towards uniformity, given that the quotient between variance and mean was always below 1 (Table 1), although the Kolmogorov-Smirnov test did not detect deviations from the Poisson distribution; and predation was extremely intense (no trays survived more than 2 days). For the 3 scrubland plots, the situation was exactly the opposite: the distributions were overdispersed and significantly distanced from the Poisson. Predation was more moderate in this type of system, with cases of bait trays which were not discovered in the course of the 75 day experiment. When dry habitats were considered alone, there was a significant effect of the system type on seed predation risk in favour of grasslands (F = 7.824; p = 0.049).

Classifying the bait trays from the 3 scrubland plots as *under shrub* vs. *open*, we found a significant effect of this factor on survival time in two of them, although with opposite signs (Table 2).

Table 1. Result of Kolmogorov-Smirnov fit tests on Poisson distribution using the survival time of the bait trays in dry habitats for each of the 6 experimental plots used in this analysis. $^*P < 0.05$; $^{**}P < 0.01$

System type	Plot	N trays	Range, days	Mean	Var/Mean	Kolmogorov-Smirnov d
Grassland	1	12	1–2	1.4167	0.186	0.17054
Grassland	2	17	1–2	1.0588	0.056	0.22704
Grassland	5	15	1–2	1.1313	0.236	0.24648
Scrubland	1	27	1–6	1.5556	1.253	0.27540 *
Scrubland	2	22	1–45	7.1364	10.265	0.42507 **
Scrubland	4	25	1–15	2.5200	4.104	0.39678 **

Table 2. Effect of presence/absence of shrub on the inverse of the survival time of the baits, detected via a *t*-test for the dry and open habitat of each scrubland plot. $^*P < 0.05$

Plot	Mean		*t*-value	df	*P*
	Under shrub	Outside shrub			
1	0.9667	0.7555	2.0657	25	0.0493*
2	0.9585	0.5451	–2.1797	20	0.0414*
4	0.8148	0.7000	0.7716	23	0.4482

Discussion

Nest-hole distribution

Messor barbarus is the main harvester ant in both system types, although *M. bouvieri* is also relatively abundant in scrubland. In this type of system the two species show a certain partitioning of the territory for nesting: *M. bouvieri* clearly prefers dry zones, while *M. barbarus* is also established in subhumid habitats. The moister areas are negatively selected by *M. barbarus*, and totally avoided by *M. bouvieri*.

This segregation between *M. barbarus* and *M. bouvieri* could be based on different requirements for nesting. Associations between nest position and certain physical soil characteristics have been found in many ant species (Sudd and Franks, 1987; Hölldobler and Wilson, 1990; Dean et al., 1997). Shrubs and rocks are often used by ants for heat regulation (Briese, 1982; Rissing, 1988; Sudd and Franks, 1987; Díaz, 1991). One of the main features of the dry zones in the analysed scrublands is precisely the abundance of small shrubs, mainly *Lavandula stoechas*, which may fulfil this heat regulation role. The overall woody species cover in this habitat type is around 40% of the soil area (Azcárate and Peco, unpubl. data), with 77% of monitored *M. bouvieri* nest-holes found under a shrub in comparison to 40% for *M. barbarus* (only considering those in dry scrubland). This may well reflect the tendency of the former species to nest beneath woody species and a degree of indifference by the latter. If this is the case, the low *M. bouvieri* density in grassland could be explained as a mere consequence of the lack of camephytes in this system. However, we do not know to what extent this segregation for nesting could also be a consequence of possible exclusion interactions between the two species, a common phenomenon amongst seed harvester ants (Whitford et al., 1976; Brown and Davidson, 1977; Gordon, 1991; Gordon and Kulig, 1996).

Both species rejected the areas under the tree canopy for nesting. The shading effect of vegetation can affect ant nesting in several ways, either promoting or restricting the establishment of ant colonies (Doncaster, 1981; Hölldobler and Wilson, 1990; Díaz, 1991). In our case it is not clear whether the low density of nest holes under the trees is motivated by the need for a degree of insolation for colony activity, or is rather a consequence of its presumable low trophic value.

Foraging areas

In spite of the infrequency of nests in moist zones, the network of *Messor barbarus* trails does enter this habitat type with even more intensity than in dry and subhumid habitats. Moist zones of both grassland and scrubland are high seed production habitats (see Methods), which may explain this result as a consequence of the reported tendency of harvester ants to forage on areas of high resource availability (Rissing and Wheeler, 1976; López et al., 1993b; but see Wilby and Shachack, 2000). On the other hand, the vegetation density is much greater in the moist patches, which probably requires the construction of cleared pathways for an efficient exploitation of this habitat type. In fact, the higher presence of trunk trails in moist habitats does not imply higher seed predation risks.

It seems unlikely that *M. bouvieri*, with temporary, less well-defined and considerably shorter trails (4–5 m, Cerdá and Retana, 1994) than those of *M. barbarus*, is able to forage in moist patches from its nests in dry habitats. *M. barbarus*, which can move more than 30 metres from its nest (Cerdan, 1989), is capable of exploiting both the moist patches where it avoids competition against *M. bouvieri* and also dry zones. Thus, dry scrub is the only habitat shared by both species to obtain resources. The differences in the foraging strategy of the two species could facilitate this coexistence, as in other areas where more than one *Messor* species cohabit (Retana and Cerdá, 1994).

As in the case of nest-holes, shaded habitats also seem inappropriate for foraging by harvester ants in both scrubland and grassland. The presence of *Quercus ilex* heavily affects the vegetation under the canopy (Bernáldez et al., 1969), leading to a more sparse plant community, with a lower seed production. In addition, even if these habitats had a high trophic value, harvester ant activity would probably be restricted by the low temperature conditions created by the tree shade.

Seed predation risk

It is important to bear in mind that the predation risk for a given seed in the field depends on its abundance and traits and also on the availability of other types of prey (Whitford, 1978; Briese and Macauley, 1981; Hobbs, 1985; Veech, 2000; Wilby and Shachack, 2000; Willott et al., 2000). Our measurements used standard seeds which are probably more attractive to ants than those in the field, and, given their non-native status, could be left in equal, controlled densities in all habitats. Our conclusions thus refer to habitat types and should not be extrapolated to particular seed species.

The experiments yielded the same spatial patterns as the foraging areas and nest-holes, thus confirming a heavy dependence on habitat type. Seed predation risk was lower under the tree canopy in both grassland and scrubland. Along the moisture gradient, the seed predation risk was practically uniform in grassland, while in scrubland the concentration of *M. barbarus* nests in the subhumid zone was probably the reason for the higher levels found in this habitat type.

At the intra-habitat scale, dry scrubland has a more heterogeneous predation pattern than dry grassland, implying the existence of small refuge areas that are safe from the action of harvester ants. In the light of the inconsistent *t*-test results, we were unable to link this effect directly to the location of *Lavandula* shrubs. The harvester ant nest and trunk trail distribution, in same cases clumped (Cerdá and Retana, 1994), might be thought to shape an overdispersed pattern of seed predation. However, we lack sufficient information to evaluate the spatial distribution of nests and trunk trails at this scale, and thus cannot confirm whether the seed predation risk follows a pattern defined by some factor outside the scope of this research. There are more parameters in which scrublands tend to be more heterogeneous than grasslands, including vegetation structure, floristic composition (Traba, 2000) and microhabitat diversity (Hobbs and Mooney, 1986), which may be linked to the homogenising role attributed to grazing at certain spatial scales (Malo and Suárez, 1996; Ramírez-Sanz et al., 2000).

In summary, our results document two different models of territorial exploitation by harvester ants. In grassland, seed predation is mainly done by one species, *M. barbarus*, which exploits all open habitats in a uniform way. In scrubland, seed predation is shared amongst two species, *M. barbarus* and *M. bouvieri*, which show a degree of spatial segregation in both nesting and foraging, and seed predation risk is distributed more heterogeneously than in grassland. Further experimental data are still needed to elucidate the mechanisms underlying these patterns, in particular the spatial segregation between the two species found in scrubland.

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