

Interspecific space partitioning during the foraging activity of two syntopic species of *Messor* harvester ants

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Terrestrial organisms can adopt different spatial strategies that range from absolute territoriality to complete spatial overlap. In ants, several theoretical models have been proposed to predict some aspects of territory formation such as the size-shape or the position of boundaries along the foraging areas of neighbouring colonies. In the present study we investigated the space partitioning during the foraging activity of two sympatric species of harvester ants (*Messor wasmanni* and *M. minor*). Colonies of the two species showed a strong territoriality with different levels of spatial overlapping in different seasons. Colonies may have reduced the cost of territorial dispute by not insisting on the same areas. Encounters between foragers belonging to interspecific colonies did not increase the probability of workers coming back to previously visited areas during the different seasons. Moreover, the evaluation of microhabitat features of foraging areas visited by the two species showed clear differences. Ecological implications and possible explanations of such space partitioning are discussed.

Key words: spatial strategies, syntopic species, *Messor wasmanni*, *Messor minor*, Ellenberg bio-indication model.

INTRODUCTION

Space, time and food are the three major resources that coexisting species could partition to reduce the effects of competition (Schoener, 1974). Space partitioning among interspecific ant colonies represents one of the most direct consequences of competition and depends largely on the foraging strategies adopted by ants (Hölldobler & Wilson, 1990; Acosta *et al.*, 1995). The distribution pattern of colonies has been also considered as a strategy adopted by species for maintaining exclusive foraging areas (Bernstein & Gobeil, 1979; Harrison & Gentry, 1981).

The size and the shape of the foraging area that territorial species may monopolize are linked to several parameters such as the distance from the central-place, the resources distribution, abundance and

stability, the worker numbers and hence the competitive ability of neighbouring colonies or, more in general, the costs and benefits of territory formation and maintenance (Gordon, 1995; Tschinkel *et al.*, 1995; Adams, 1998; Brown & Gordon, 2000; Adams, 2001; Adams & Tschinkel, 2001; Adams, 2003; Adler & Gordon, 2003; Both & Visser, 2003).

Harvester ants, especially common in arid and semi-arid environments, show a different food choice based on seed size and shape or food-handling capacity (Pulliam & Brand, 1975; Morehead & Feener, 1998; Detrain & Pasteels, 2000; Willot *et al.*, 2000; Pirk & Lopez de Casenave, 2006; Solida *et al.*, 2007). The foraging strategies of harvester ant species include individual foraging and the development of complex trunk trail systems with different species exhibiting a variety of territorial behaviours (Hölldobler & Wilson, 1990; Baroni Urbani, 1991; Acosta *et al.*, 1995; Gordon, 2002).

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The territory of a harvester ant colony has been considered as an example of stable territorial systems (Krebs & Davies, 1984; Hölldobler & Wilson, 1990). On the timescale of days and weeks, colonies may use different trunk trails, the direction of which depends on the foraging behaviour of neighbours and on the availability of resources (Gordon, 1991, 1992). The trunk trail systems usually diverge and channel the mass of foragers of neighbouring interspecific, and also intraspecific, nests in different directions. This system can be considered as an adaptive strategy adopted by species to partition space and to reduce the cost of aggressive encounters between neighbouring colonies (Hölldobler, 1976; Davidson, 1977; López *et al.*, 1993; López *et al.*, 1994). Generally, low levels of overlap in the foraging range of colonies are expected in harvester ants. Active defense of territories, avoidance of conflicts with neighbouring colonies and the exploitation of resources are the mechanisms proposed to explain such a low level of overlap (Acosta *et al.*, 1995; Gordon & Kulig, 1996; Adler & Gordon, 2003). Moreover, territory size and territorial behaviours may also change during the ontogeny of territory owners (Gordon, 1995).

Messor wasmanni and *M. minor* are typical seed-harvester ants especially common in Central-Southern Italy where they can often, but not always, be found in strict syntopic conditions (Baroni Urbani, 1971; Poldi *et al.*, 1994; Solida *et al.*, 2007). *Messor minor* is generally present, with different subspecies, in the Mediterranean Basin, Canarias and in Asia up to Turkestan; *M. wasmanni* has a Mediterranean and Central-Asiatic distribution (Bernard, 1968; Baroni Urbani, 1971). The two species are different in size; *M. wasmanni* is in average larger (workers length 3–9.5 mm) than *M. minor* (workers length 3.5–8 mm) and with a higher level of polymorphism among its workers (Bernard, 1968; Baroni Urbani, 1971). The biology of the two species has only occasionally been studied and only few reports on some aspects of their behavioral and foraging ecology are available (Harkness & Isham, 1988; Grasso *et al.*, 1999, 2004; Solida *et al.*, 2007). In some areas of central-southern Italy colonies of the two species may form dense populations coexisting in the same areas. Colonies generally dwell in single nests but at least for *M. wasmanni* a slight polydomy is possible (Harkness & Isham, 1988; pers. obs.).

In this study, we aimed to investigate the interspecific space partitioning promoting the coexistence between colonies of the two species of *Messor* harvester

ants (*Messor wasmanni* and *M. minor*). To underline the factors that could promote this space partitioning, the following four questions were raised:

1. which was the spatial distribution of nests of the two species?
2. did colonies utilize exclusive or overlapping areas during the sampling periods?
3. could the amount of interactions of heterospecific workers at impinged foraging areas affect the probability for the ants to return to the same areas?
4. did plant community composition promote an interspecific space partitioning?

MATERIALS AND METHODS

Study site

The study was performed in a typical grassland area, called “Coltivati”, inside the Natural Reserve of the Presidential Estate of Castelporziano (near Rome, Italy). The Estate, ~6200 ha, is located along the Tyrrhenic coast in Central Italy and is characterised by a xeric region climate, inferior Mediterranean thermotype. Rain precipitations range from 129 mm (November) to 12 mm (July) and air temperature ranges from 4 °C (January) to 30 °C (July) (data provided by the Castelporziano meteorological station). The soil is mainly sandy and of alluvial nature with both recent and ancient dune formations (Pinzari *et al.*, 2001). The typical vegetation is composed of herbaceous plants, such as *Dasyphyrum villosum* (Poaceae) and *Vulpia ligustica* (Poaceae), belonging to xeric Mediterranean grasslands and considered as a single phytosociological association referred to as “*Vulpia ligusticae-Dasyphyretum villosi*” (Fanelli, 1998; Pignatti *et al.*, 2001).

Sampling protocol

Previous observation showed that ant colonies were equally present in all Coltivati area (Fanfani *et al.*, 2006).

Messor wasmanni and *M. minor* exhibited a pattern of foraging behaviour common to several harvester ants that includes searching for food along well defined trunk trails at the end of which the workers disperse in a “fan” (*sensu* Brown & Gordon, 2000). The colonies of both species were able to produce more than one column during the day, especially *M. wasmanni*, which had generally bigger colonies with respect to *M. minor* (pers. obs.).

To study the space partitioning between coexisting species we first delimited at random a grid of 30 m × 30 m divided in 900 plots of 1 m² each, inside the Coltivati area. All nests present in these areas were detected and mapped (15 nests of *M. wasmanni*; 18 nests of *M. minor*). Data were collected during three 10-day periods in May, July and October respectively, to cover the whole foraging season of these species.

To detect the spatial distribution of colonies we measured the minimum distance between the colonies, at intra- and interspecific level and irrespective of direction, inside the delimited grid used for a “Nearest Neighbor Analysis” (see below).

To note if colonies gain exclusive or overlapped territories we first mapped the “daily foraging area” covered by colonies during the sampling periods. This area is composed not only of the foraging fans (Brown & Gordon, 2000) but also by the different plots crossed in one day by active trunk trails. Each colony was observed twice during each sampling day to map the maximum area covered. In this way, for each 10-day period, the mean dimension of the daily foraging area represented the average number of plots visited by each colony. We have excluded from the analysis all nests where workers were engaged in foraging trips outside the delimited grid.

To detect if the amount of interactions at fans between heterospecific workers affected the probability of foragers coming back to the same area, the numbers of impinged fans during each sampling period was recorded. The same subset of colonies already studied has been used for this purpose.

Finally, to understand if possible differences in the plant community composition at fans promoted a space partitioning between colonies of the two species, in a subsample of fans (89 for *M. wasmanni* and 59 for *M. minor*), all the plant species and relative percentage of coverage was recorded.

The data allowed us to apply the Ellenberg bio-indication model (EBM) (Ellenberg, 1979; Pignatti et al., 2001). The model represents not only an easy way to interpret the vegetation patterns in terms of ecological factors, but moreover, as long as it represents the realized niche of species, it allows us to assess the ecological factors from the perspective of the plants. The model assigns to each plant species the value of five ecological parameters (Ellenberg indicator values, EIV), that together represent the overall requirements of a plant to grow on a specific soil: light (L), temperature (T), soil moisture (F), soil pH and nitrogen (N). In the application of EBM, we transformed

the plant species data and relative percentage of coverage, obtained by phytosociological sampling, in the weighted mean of each EIV according to:

$$\frac{\sum (i \times x_i)}{\sum x_i}$$

where x_i represents the plant coverage in the fan and i the relative EIV. EBM allows us to detect small differences within a homogeneous habitat characterized by only one plant community association, as in our research. Limitations and strengths of the Ellenberg approach have been debated, but many studies show a good concordance between indicators and environmental variables (Ewald, 2003).

Statistical analysis

In order to investigate the spatial arrangement of colonies at both intra- and interspecific levels, a “Nearest Neighbor Analysis (NNA)” was preliminary performed. The degree to which the observed distribution departs from random expectation with respect to the distance to nearest neighbour is given by the value of R . When R does not significantly differ from 1, nests follow a random distribution, when $R < 1$ nests are clumped and when $R > 1$ nests are overdispersed (Clark & Evans, 1954). The Donnelly (1978) correction has been applied to take into account the edge effect and the number of nests inside the area less than 100 units.

To verify if interspecific colonies present a partial overlapping or an exclusive use of space during the three seasons (May-July-October), we used the “asymmetrical weighted overlap values” (Smith & Dobson, 1994). The weighted “overlap value” of one species relative to the other is the proportion of the total area occupied by a species that is shared with the other during a considered period:

$$\text{Overlap} = \frac{[\text{total use (in days) of all plots that species 1 (} M. \text{ wasmanni) shared with species 2 (} M. \text{ minor)}]}{[\text{total use (in days) of all plots used by species 1}]}$$

Moreover, a two-way ANOVA has been used to check for differences in the dimension of the daily foraging areas occupied by the two species. We also considered the effect of the seasons (May-July-October) on the dimensions of the daily foraging area by means of Scheffé test for *post hoc* comparison. To meet the assumption of homoscedasticity, ANOVA was performed on log-transformed data and on random subsamples of the same size (balanced analysis) for each species.

To determine if the amount of encounters at fans during the different sampling periods affected the probability of workers returning to previously visited fans, the Kolmogorov-Smirnov test was applied. Finally, the Mann-Whitney U test has been used to verify that space partitioning was promoted by differences in the plant community composition at fans strictly linked to the five Ellenberg indicator values.

RESULTS

Nest distribution

The Nearest Neighbor Analysis (NNA) showed that the colonies of each of the examined species followed a random distribution (*M. wasmanni*: $R = 1.12$, $p = 0.41$; *M. minor*: $R = 0.86$, $p = 0.26$). However, when R value was computed putting together the distribution of all nests present in the grid, the spatial arrangement of colonies turned from random to overdispersed ($R = 1.18$, $p = 0.05$).

Asymmetrical weighted overlap values

The colonies of *M. wasmanni* (15) shared with *M. minor* 2.73% of their total foraging areas in May, 12.52% in August and 7.53% in October. *Messor minor* colonies (18) shared with *M. wasmanni* a greater proportion (almost double) of their foraging areas, in all data sampling steps: 5.86% in May, 22.79% in August and 14.49% in October. Hence, the two species showed the same trend across the foraging season sharing the greater proportion of their foraging area in August, less in October and even less in May.

Daily foraging area

The daily foraging areas gained their maximum extension during the summer period (Aug) for both species and remained quite extensive at the end of the season (Oct) in respect to the beginning (May).

TABLE 1. Results of the two-way ANOVA based on the differences in the mean dimension of the daily foraging area visited by the two species (species, months and species \times months interaction)

	df	MS	F	<i>p</i>
Species	1	19.96	170.22	<0.001
Months	2	38.31	326.69	<0.001
Species \times Months	2	1.66	14.14	<0.001
Error	390	0.12		

Messor wasmanni daily foraging area in m^2 (mean \pm SE): 4.08 ± 0.77 (May), 13.21 ± 0.87 (Aug), 4.82 ± 0.45 (Oct); *M. minor* daily foraging area in m^2 (mean \pm SE): 1.54 ± 0.18 (May), 6.43 ± 0.56 (Aug), 3.53 ± 0.34 (Oct). Since the homoscedasticity hypothesis has been verified (Bartlett test = 8.55, $p = 0.128$, $df = 5$), ANOVA was performed. Results showed a significant difference in the mean dimension of the daily foraging area visited by the two species. There was also a significant effect of seasons (months) and in the interaction of species with months (Table 1).

In all sampling periods (May-Jul-Oct), *M. wasmanni* colonies exploited significant larger areas compared to *M. minor*. For *M. wasmanni*, significant differences in the size of the daily foraging area visited by intraspecific colonies emerged (comparing May to July and July to October). For *M. minor*, differences occurred in all cases (May vs July, May vs October, July vs October) (Table 2).

We recorded the different sampling periods encounters at fans between non-nestmate foragers of interspecific colonies. The total number of encounters was (mean \pm SE): 0.4 ± 0.16 in May, 4.7 ± 0.54 in July and 1.6 ± 0.37 in October. Significant differences occurred in the amount of encounters across the sampling months (t-test for independent samples, $df = 18$): $t = -7.64$, $p < 0.001$ (May vs August); $t = -2.96$, $p < 0.01$ (May vs October); $t = 4.74$, $p < 0.001$ (August vs October).

TABLE 2. Scheffé test for *post hoc* comparison (Error: Between MS = 0.033, $df = 46$) between the dimensions of the daily foraging area exploited by the two species in all sampling periods

Species	Month	1	2	3	4	5	6
1 <i>M. minor</i>	May		0.000	0.000	0.000	0.000	0.000
2 <i>M. minor</i>	July	0.000		0.000	0.001	0.000	0.639
3 <i>M. minor</i>	October	0.000	0.000		0.979	0.000	0.026
4 <i>M. wasmanni</i>	May	0.000	0.001	0.979		0.000	0.131
5 <i>M. wasmanni</i>	July	0.000	0.000	0.000	0.000		0.000
6 <i>M. wasmanni</i>	October	0.000	0.639	0.026	0.131	0.000	

Most fans were visited by the foragers of the two species only once during each sampling period (Fig. 1). Conversely, the number of days in which a fan was visited by the workers of *M. wasmanni* and *M. minor*

did not depend significantly on seasons. The frequencies of use of fans by each species remained in fact the same in all sampling periods (Kolmogorov-Smirnov test, $p > 0.1$, all comparisons among months).

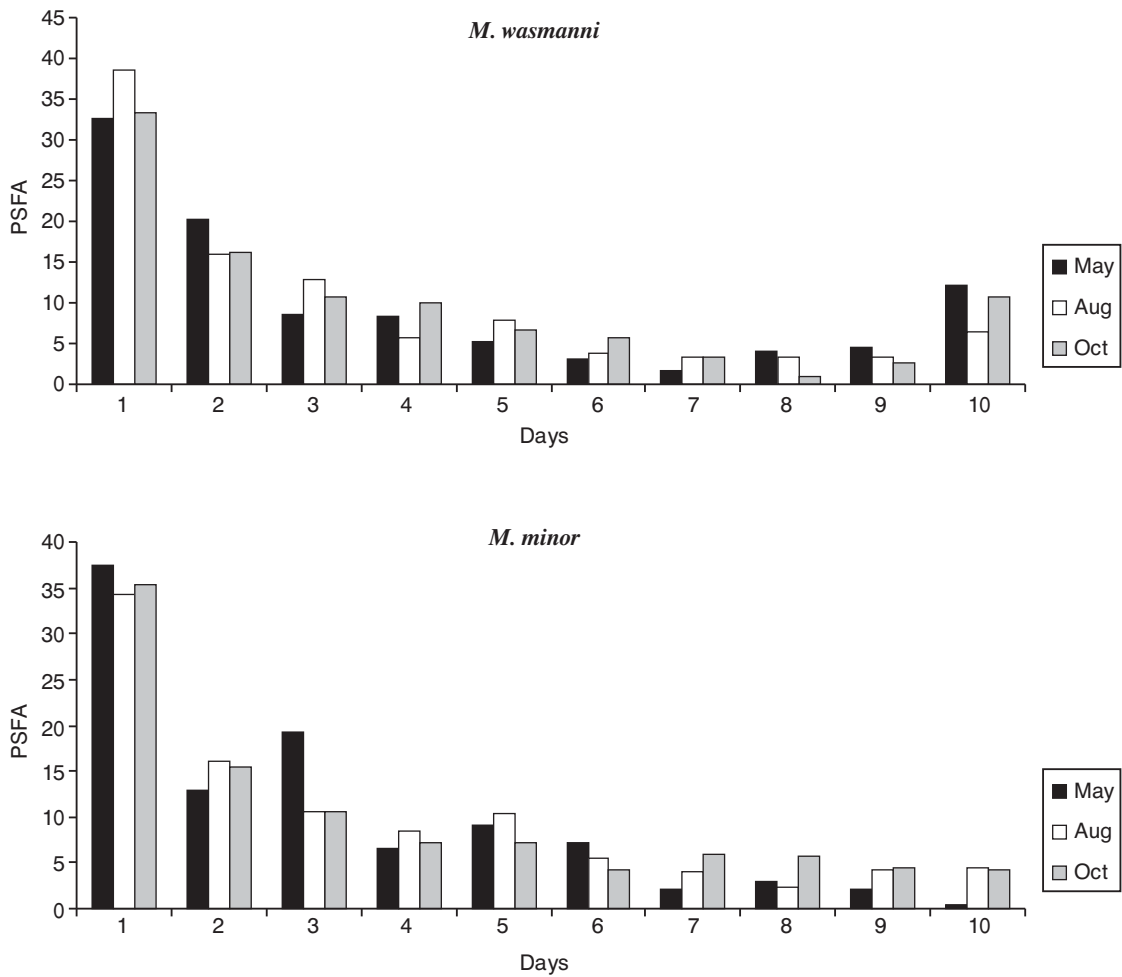


FIG. 1. Percentage of seasonal fans (PSFA) visited by the workers of the two ranging from 1 to 10 times during each sampling period. Data show that in most cases the workers tended to visit a fan only once. No differences emerged comparing the percentage of fans visited by the workers of each species during the months (Kolmogorov-Smirnov test, see text).

TABLE 3. Differences in the characteristics of the fans visited by the two species in the whole foraging season described by means of the application of the Ellenberg bioindication model (EIV: Ellenberg indicator values; N: sample size)

EIV	<i>M. wasmanni</i>			<i>M. minor</i>			Mann-Whitney U test	
	mean	SD	N	mean	SD	N	U_p	
pH	5.82	0.16	252	5.82	0.18	340	34222.00	< 0.001
N	4.98	0.36	252	4.99	0.29	340	36909.00	< 0.010
F	3.41	0.24	252	3.36	0.16	340	34791.50	< 0.001
T	6.54	0.21	252	6.56	0.20	340	34271.50	< 0.001
L	8.01	0.03	252	8.01	0.03	340	36948.00	< 0.010

Ellenberg bioindication model

At the end of the foraging season we obtained 89 plots crossed by fans for *M. wasmanni* and 59 for *M. minor* characterized at the fine microhabitat level by means of the Ellenberg bioindication model. The comparative analysis of the five ecological parameters (L - T - F - N - pH) included in the model showed that the workers of *M. wasmanni* and *M. minor* foraged on sites where Ellenberg indicator values, and hence the plant community composition, were statistically different (Table 3).

DISCUSSION

Interspecific colonies of the two *Messor* harvester ants considered in this study exhibited characteristics that are generally accepted as indicators of competition: regular spatial distribution and, on a daily scale, the utilization of exclusive foraging areas (Bernstein & Gobbel, 1979; Harrison & Gentry, 1981; Acosta *et al.*, 1995; Gordon & Kulig, 1996; Adler & Gordon, 2003).

The spatial arrangement of colonies can be considered one of the results of interactions among species (Clark & Evans, 1954). In areas where environmental resources are aggregated, colonies tend to develop a clumped distribution to maximize exploitation of territory (Czechowski, 1975). The same pattern is expected in polydomous species, since habitat exploitation per colony increases linearly with nest number (Cerdá *et al.*, 2002). For *M. wasmanni* we occasionally observed the presence of subsidiary nests and hence slight evidence of polydomy, as reported for a population of the same species in Greece (Harkness & Isham, 1988). To explain the random distribution of nests at intraspecific level we can suppose that environmental resources were equally distributed in the studied area. The irregular shapes of the two syntopic colonies foraging ranges could allow them to partition space even though the nests were randomly distributed (Gordon, 1995). In this way, chemical-physical proprieties of the soil could be crucial in determining the distribution and abundance of ant nests (Johnson, 2000; Cerdá, 2001). When competition for resources is strong, colonies tend to maximize the mean distance between nests (overdispersion), reducing the overlap of foraging territories (Bernstein & Gobbel, 1979; Cushman *et al.*, 1988). We recorded that the overall distribution of nests of the two examined species was overdispersed and this fact probably means that one of the strategies to promote space partitioning, coexistence and to reduce compe-

titution was to maximize the distance of interspecific colonies (Harrison & Gentry, 1981; Ryti & Case, 1986; Acosta *et al.*, 1995; Gordon & Kulig, 1996; Adler & Gordon, 2003).

In ants, a territory is an area occupied more or less exclusively by a colony by means of repulsion of intra- and interspecific competitors through overt defence or aggressive display. Territorial strategies range from absolute territoriality, when a species defends permanently the foraging area, the nest sites or any other resource (exclusive territory), to complete spatial overlapping (Levings & Traniello, 1981; Hölldobler & Wilson, 1990). Our results suggested that territoriality between colonies of the two considered species was strongly developed (Hölldobler, 1976; Davidson, 1977). On a daily scale, the trunk trail systems adopted by both species could be considered very effective in space partitioning (Harkness & Isham, 1988; López *et al.*, 1993, 1994; Acosta *et al.*, 1995; Gordon, 1995). On a seasonal scale, colonies of both species did not always conserve previous visited territories. Probably, when a foraging area becomes less attractive as resources become less abundant, and the rate at which successful foragers come back to the nest decrease, colonies tend to exploit a new sector of the foraging area changing the foraging direction (Rissing & Wheeler, 1976).

Messor wasmanni foragers were able to exploit larger areas in all sampling occasions compared to *M. minor* workers probably because, as in the case of *Solenopsis invicta* (Tschinkel *et al.*, 1995), its colonies generally have larger worker population and hence a higher fighting ability (pers. obs.).

Our results also highlighted that significant differences in the average dimension of the territory visited by each species occurred across seasons. The main factors that control territory size are the availability of resources, the fighting ability of neighbour colonies and the task performed by foragers in the considered period (Gordon, 1995; Adams, 2003). At the beginning of the foraging activity (May), workers employed energies to clear from vegetation and other obstacles the trunk trail systems to reduce the time spent in foraging trips (López *et al.*, 1993). The minimum size of territories observed in May could also be due to the fact that during this month the workers population of colonies, after the winter hibernation period, probably reached its annual minimum (Tschinkel *et al.*, 1995). During the production and maturation of reproductives (July), colonies would increase the food intakes exploiting bigger territories, since

males and queens are larger than workers and require more food (Tschinkel, 1993; Adams, 2003). Moreover, in this period the availability of resources reached its annual peak, since almost all seeds are on the ground. An opposite situation occurred in October when resources were increasingly scarce on the ground.

As colonies exploited larger foraging areas, they are likely to impinge on the fans of their neighbouring societies more frequently (Brown, 1999; Brown & Gordon, 2000). Our results regarding the amount of encounters at fan between foragers belonging to interspecific colonies reflected seasonal changes in the size of the daily foraging areas exploited by the two species.

Nevertheless, the number of encounters among heterospecific colonies was very low during all sampling periods. Probably the development of the trunk trail systems and the consequent use of exclusive foraging areas by each colony, as well as the overdispersed nests distribution, minimized the amount of encounters with neighbouring heterospecific foragers (Harrison & Gentry, 1981; Harkness & Isham, 1988; Gordon & Kulig, 1996; Brown & Gordon, 2000).

Encounters at fans could affect the foraging activity of ants in two ways: 1) workers might avoid foraging at encounter sites in order to minimize the cost of competition and 2) workers might prefer to return to these sites to defend territorial boundaries (Gordon & Kulig, 1996; Brown & Gordon, 2000). As it was also reported by Brown & Gordon (2000) for *M. andrei*, most fans were visited by the foragers of the two species for only one day during each sampling period. Nevertheless, the rate at which ants returned to the same fans did not change over time, suggesting that differences in the amount of encounters between heterospecific colonies did not alter the probability that space was revisited by interspecific foragers at the seasonal scale. Probably, fighting interactions tend to affect the distribution of foraging activity of competitors, especially when the benefits of the monopolization of an area are low if compared with the cost of fighting (Brown & Gordon, 2000; Stamps & Krishnan, 2001; Morrell & Kokko, 2003, 2005). In this way, if neighbouring societies avoid each other to reduce the energetic cost of fighting, a sort of “dear-enemy phenomenon” could be invoked to explain our results (Fisher, 1954; Harkness & Isham, 1988; Gordon, 1989; Langen *et al.*, 2000). In this context, the trunk trail systems adopted by myrmicine harvester ants are extremely functional in promoting such space partitioning (Hölldobler & Wilson, 1990; López *et al.*, 1993;

Acosta *et al.*, 1995). Systems of colony area (nest and trunk-trails) recognition based on chemical labels with colony specific markers have been studied in several ant species including *Messor* ants, providing a proximate explanation of mechanisms favouring space partitioning and avoidance of already occupied areas (Gordon, 1984; Hölldobler & Wilson, 1990; Trianiello & Robson, 1995; Grasso *et al.*, 2000, 2005).

Competition among harvesting ants species is intense and can lead to resource partitioning along spatial and temporal gradients, or to the utilization of seeds of different sizes and of different density distribution (Davidson, 1977; Harrison & Gentry, 1981).

Although our study has been conducted within a grassland area (Coltivati) belonging to *Vulpio ligusticae-Dasypyretum villosi*, the EBM represents a very effective tool able to underline at 1 × 1 m scale small heterogeneities in the plant community composition. Differences in the mean values of the five ecological parameters included in the model reflect differences in the plant community composition at the microsite levels. Therefore, the distribution of seeds of actively exploited plants could affect the foraging patterns of the two examined *Messor* species and promote the highly observed level of space partitioning. This aspect could be also the basis for a possible diet segregation between the two syntopic ant species. Further investigations will be focused on this aspect to underline possible mechanisms in promoting a niche shift and the coexistence of the two species in strictly syntopic conditions.

Finally, the interspecific space partitioning between the two harvester ants here considered could also reflect a “trade-off” between interference-exploitation abilities. Coexistence could be in fact favoured if the subordinate species adapts itself to forage in less favourable microhabitats, driven out from the high quality territories by the dominant *Messor* harvester ant (Savolainen & Vepsäläinen, 1988; Cerdá *et al.*, 1997; Dietrich & Wehner, 2003).

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