

Consequences of behavioral vs. numerical dominance on foraging activity of desert seed-eating ants

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Abstract Dominance relationships among species play a major role in the structure of animal communities. Yet, dominant species with different trade-offs in resource exploitation and monopolization could affect community structure in variable ways. In ants, dominant species could be classified into either behavioral dominants that exhibit territorial aggression or numerical dominants that exhibit high biomass or frequency of occurrence. While each class of dominance has generally been found to negatively affect the foraging activity of species in ant communities, the concurrent effect of both classes of species has never been tested. Here, we examined the effects of two behaviorally dominant species, *Crematogaster inermis* and *Monomorium salomonis*, and a numerically dominant species, *Messor arenarius*, on the foraging behavior of seed-eating species in a desert ant assemblage. In a 1-year study, the foraging activity of the ant species was assessed using seed baits, which were sampled during night and day. While the numerically dominant species exhibited high foraging efficiency and negatively affected the ability of other seed-eating species to obtain seeds, significantly more seeds remained at baits that were occupied the previous night by each of the two behaviorally dominant species, possibly due to

aggressive exclusion of *M. arenarius* foragers from the baits. This exclusion also facilitated greater foraging activity of the seed-eating species. Our results demonstrate how these two types of dominance could differently affect the foraging activity of ant species in the community.

Keywords Ants · Desert granivores · Dominant species · Exploitation competition · Foraging behavior · Interference competition

Introduction

Interspecific competition has long been considered as an important process determining the structure of ecological communities (MacArthur 1972; Diamond and Case 1986; Chase and Leibold 2003). Interspecific competition may affect the behavior and abundance of species within the community as well as alter the dominance relationships among them (e.g., Gause 1935; Connell 1961; Tilman et al. 1981; Whittam and Siegel-Causey 1981; Vahl et al. 2005). These competitive interactions may be either direct behavioral interferences (e.g., territoriality, aggressiveness, etc.) or indirect, via the exploitation of limited resources. Yet, the ecological conditions under which competition between species influences the structure of communities are still unclear. Specifically, it is important to recognize the varying effects of species that differ in ecological traits, such as in their abilities to discover, exploit, or monopolize resources (Chase et al. 2001; McGill et al. 2006; Adler et al. 2007). Such interspecific trade-offs in ecological traits could permit the coexistence of species, particularly at small spatial scales (MacArthur 1972; Tilman 1982). To date, however, examination of the role of species with different

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life-history traits in the structure of natural communities is lacking.

In ants, territorial aggression between species frequently leads to the organization of communities into dominance hierarchies (Wilson 1971; Savolainen and Vepsäläinen 1988; Andersen 2000), whereby ant species can be classified into either subordinate species or behaviorally dominant species, which display aggressive behavior eliciting avoidance behavior in other species (Cerdá et al. 1997; Davidson 1998; Parr and Gibb 2010). This classification provides excellent opportunities to examine the effects of aggressive behavior and interference competition on community structure (e.g., Hölldobler and Wilson 1990; Morrison 1996; Gotelli and Arnett 2000; Sanders and Gordon 2003; Gibb and Hochuli 2004; Sanders et al. 2007). For example, behaviorally dominant ant species have been shown to affect community structure by competitively excluding the activity of foragers of subordinate species (e.g., Andersen and Patel 1994; Vepsäläinen et al. 2000; Sanders and Gordon 2003) or of other dominant species (e.g., LeBrun et al. 2007).

Within ant communities, dominance has been found to be negatively correlated with ant species richness (“dominance-impoverishment rule,” Hölldobler and Wilson 1990). Accordingly, communities with low species richness are more likely to be behaviorally dominated by one or a few species with large, aggressive colonies that maintain exclusive territories, a pattern which could be attributed to negative effects of the dominant species, such as competitive exclusion (Hölldobler and Wilson 1990; Parr 2008). In addition to the behaviorally dominant species, ant communities may also be affected by numerically dominant species (Davidson 1998; Parr and Gibb 2010). Such species are dominant in terms of biomass or frequency of occurrence, rather than aggressive behavior and may affect other species within an ant community through rapid discovery and depletion of food patches before they can be located by other species (e.g., Human and Gordon 1996; Adler et al. 2007). Numerically dominant species are therefore likely to have a negative effect on ant communities through exploitative competition.

While in some ant communities the behaviorally dominant species are also numerically dominant (e.g., Porter and Savignano 1990; Andersen and Patel 1994; Human and Gordon 1996; Morrison 1996; Santini et al. 2007; Arnan et al. 2011), in others a “dominance-discovery trade-off” (sensu Fellers 1987; Davidson 1998; Parr and Gibb 2010) prevails, according to which species that are more efficient in resource discovery and exploitation are the less aggressive ones (e.g., Fellers 1987; Holway 1999; LeBrun and Feener 2007; Feener et al. 2008). If such a trade-off exists within a community, behaviorally and numerically dominant ant species would differ in ecological traits, such as resource exploitation and interference, and could thus differentially

affect the foraging activity and abundance of other species within the community. Although several studies have examined the separate effects of either the behaviorally or numerically dominant ant species, to our knowledge the concurrent effect of both classes of dominance on ant communities have never been tested under field conditions. In this study, we examine the interactions among multiple dominant species, with different mechanisms of dominance, behavioral vs. numerical, and their effects on the foraging behavior of ground-dwelling ant species in a desert ant assemblage.

The study was conducted using food baits in an ant assemblage in the Negev Desert of Israel. In this paper, we first show that this ant assemblage is dominated by three common species: two behaviorally dominant species, *Crematogaster inermis* (Mayr, 1862) and *Monomorium salomonis* (Linnaeus, 1758), and a single numerically dominant species, *Messor arenarius* (Fabricius, 1787). We then demonstrate the impact of either the numerically or behaviorally dominant species on the structure of this ant assemblage by exploring their effects on the foraging activity of the ground-dwelling ant species in the experimental baits, focusing on seed-eaters.

Methods

Study site

The study was conducted at Mashabim Sands Nature Reserve in the Negev Desert, Israel (31.00° N/34.43° E). This region has a Mediterranean bi-seasonal climate, with a mild and rainy winter growth season (October–March), and a warm dry summer season. Mean annual precipitation is 110 mm while average summer-maximum and winter-minimum temperatures are 33.5°C and 6°C, respectively (Israeli Meteorological Service data). The area is characterized by three habitat types: semi-stabilized dunes, stabilized sands and rocky hillsides. In order to reduce habitat heterogeneity, sampling took place only in the stabilized sands, where vegetation varies from an open grassland sparsely covered with annuals to a shrubland with patches of perennials including *Retama raetam*, *Lycium shawii*, and *Artemisia monosperma*.

Natural history of the ant species

M. arenarius is a harvester ant, foraging mainly on plant seeds but occasionally collecting other plant material and dead invertebrates. This species is highly polymorphic in its worker size (4–15 mm) and exhibit a mixed foraging strategy of both solitary and group foraging, according to the distribution of resources (Steinberger et al. 1992; Avgar et

al. 2008). This species builds large horizontal nests, which can extend for meters, providing access to a wide foraging range (Ofer 2000). *C. inermis* and *M. salomonis* are generalist seed eaters, which feed on seeds and other plant material, dead invertebrates, floral nectar and homopteran honeydew. The workers of these species are relatively small (3–4 mm) and forage in groups along pheromone-laid trails (Kugler 1989). Colonies of *C. inermis* nest inside hollow branches of perennial shrubs, such as *R. raetam* while colonies of *M. salomonis* nest in the soil.

Experimental design

The experimental system consisted of three randomly chosen 80×60 m plots, located at least 30 m apart. Each plot included 20 uniformly distributed food baits, positioned 20 m apart. The baits consisted of 4 g of millet and broken sunflower seeds of varying sizes to attract both small and large seed-eating ant species. Preliminary observations have shown that these food types were taken by all seed-eating ant species, regardless of their forager size. Although the addition of food in a clumped manner is likely to be more beneficial to species that monopolize food resources than to those which are better at detecting new food resources, the use of such baits is appropriate in desert sand habitats, where seeds are the main food resource, and these are usually found in large patches under shrubs or exposed by sand movement (Davidson 1977; Reichman 1979; Ben-Natan et al. 2004). All baits were protected by a 30-cm³ meshed wire cubic enclosure (1 cm² mesh size) whose base was buried in the sand with a tightly attached aluminum tray. This enclosure prevented both rodents and birds from reaching the seeds and ensured ants were the only granivores able to enter the baits.

Baits were observed once a month during the winter (November–March) and summer (April–September) of 2002 for a total of ten sampling days, in which each bait was visited once during both the night and the day. Seeds were placed in the baits at sunset to match the natural environment, where new food patches are exposed by sand movement at dusk. Sampling initiated 3 h following baiting for the night observations and 9 or 12 h for the day observations in the summer and winter seasons, respectively. These differences were mainly due to differences in day length as well as duration of ant activity, which is longer at winter days. The observations were conducted for a fixed time of two minutes and included counting the number of individuals that occupied the baits per species, as well as recording their behavior, which was assigned as either aggressiveness, avoidance, or stealing. The quantity of seeds remaining in the baits was ranked by a visual estimation according to five quantities from 0 (no seeds remaining) to 1 (approximately all seeds remaining). Ground temperatures

were measured during sampling using an Enviro-Safe[®] pocket thermometer (H-B Instrument Company, USA). Individuals were identified by species onsite and in cases of uncertainty were collected and identified in the laboratory.

Data analysis

The effect of season (summer vs. winter) on the foraging activity of the different species at baits was examined using repeated-measures ANOVA, in which species occupancy was the dependent factor, season, sampling day and diel patterns of activity (visits during night and day) were the within-subject factors and species was the between-subject factor. Species occupancy at the baits was calculated as the proportion of occupied baits in a plot per visit and was log transformed (species occupancy +1) to meet the assumptions of normality and homogeneity of variances (Zar 1999). The repeated-measures ANOVA assumption of circularity was tested using Mauchly's test of sphericity and was found to be valid for the within-subjects factor. Post hoc Tukey's mean comparisons were performed to reveal differences in species activity between seasons.

Temporal activity of the three dominant species was evaluated as the ground temperatures, in which 50% or more of the maximum number of foragers were active at the baits (i.e., *thermal activity breadth*, Cerdá et al. 1998). The effects of season and species on the thermal activity breadth (log transformed to ensure normality) were examined using a two-way ANOVA. Post hoc Tukey's mean comparisons were performed to reveal differences among species within season. The relationship between temperature and species activity in baits was visualized using locally weighted scatterplot smoothing (LOWESS), which provides an empirical representation of the relationship between the two variables by fitting the data within small sections based on a proportion of the data points (Legendre and Legendre 1998; Bestelmeyer 2000). In this case, the proportion was set to 0.5.

Competition intensity was determined by examining whether co-occurrence patterns among species at baits were aggregated or segregated in space using EcoSim, version 7 (Gotelli and Entsminger 2005), which tests for non-random species co-occurrence patterns in a presence-absence matrix by randomizing the original matrix and generating random matrices (5,000 in our analyses). We used the Stone and Roberts (1990) C score index, which quantifies the tendency of species to not co-occur by measuring the average number of checkerboard units (i.e., pairs of baits occupied by two different species) among the three species. In a competitively structured community, the C score should be significantly larger than expected by chance. The null model algorithm

used in this analysis consisted of equiprobable columns (samples) and sums fixed rows (species), allowing the number of species in a sample to vary while keeping the same average number of species for the samples. This null model was suggested as the most appropriate algorithm for analyzing samples such as food baits (Gotelli 2000).

Species aggressiveness was quantified by observing inter-specific interactions that resulted in either a retreat or death of individuals at baits. Furthermore, for cases in which two of the three dominant species were simultaneously present in the same bait, the correlation between densities of the two species at the bait was examined using Spearman's rank coefficient (r_s). For this analysis, we excluded baits in which none of the species were present and included only plots that were simultaneously occupied by the target species. In addition, a logistic regression test was used to examine the relationship between the density of the two behaviorally dominant species and the presence of the numerically dominant *M. arenarius* at baits. A significant relationship could suggest that the presence of *M. arenarius* is affected by the density of the two behaviorally dominant species.

Differences in foraging efficiency among the three dominant species were examined by comparing the amount of resources remaining at baits, in which the study species were exclusively present during the night. The analyses were separated for the winter and summer since during winter, *M. arenarius* is the only species active at night. Since the data could not be normalized, we used non-parametric Kruskal-Wallis tests.

To examine the effect of the dominant species' presence at baits during summer nights on the occurrence of seed-eating ant species in the same baits the following day, the baits were assigned according to the species occupying them at nights. Food baits unoccupied during the night observation were excluded from the analysis since it was impossible

to assume that these baits were not occupied during the night by any of the species. The effects of bait category on species abundance (transformed to log (abundance at bait+1)) and species number (transformed to log (species number at bait+1)) in baits during the day were tested using two separate one-way ANOVAs. Post hoc Tukey's mean comparisons were performed to reveal differences between bait categories. The effect of either the behaviorally or numerically dominant species on the other seed-eating ant species (excluding the dominants) was then examined using a Chi-square test. The observed values were the number of baits occupied during the night by one of the dominant species and by one of the other seed-eating species during the day. The expected values were calculated from the proportion of dominant species at baits during summer nights. Statistical analyses were conducted using PASW Statistics 18 (SPSS Inc., Chicago, IL).

Results

Eight seed-eating ant species were observed at the food baits (Table 1). Three of them were specialist seed-eaters: *M. arenarius*, *Messor ebeninus* (Santschi, 1927), and *Messor aegyptiacus* (Emery, 1878). The remaining five species were generalist seed-eaters: *C. inermis*, *M. salomonis*, *Monomorium pharaonis* (Linnaeus, 1758), *Pheidole pallidula* (Nylander, 1849), and *Temnothorax arenarius* (Santschi, 1908). The three most common species (i.e., occurring in at least 10% of the baits in one of the seasons) were *M. arenarius*, *C. inermis*, and *M. salomonis* (Table 1).

The effect of season on bait occupancy significantly differed among the three common species (repeated-measures ANOVA: significant species by season interaction, $F_{2, 6} = 56.12$; $P < 0.001$). While the activity of *M. arenarius*

Table 1 Species activity at the baits (max=300 baits) during the winter and summer including their thermal tolerance (ground temperature ranges in which species were active), the maximum number of foragers, and their occurrences at night and day observations

Species	Winter			Summer				
	Thermal tolerance (°C)	Max number of foragers	No. of occurrences		Thermal tolerance (°C)	Max number of foragers	No. of occurrences	
			Night	Day			Night	Day
<i>Messor arenarius</i>	6–25.5	50	205	223	10–28	45	158	154
<i>Messor ebeninus</i>	18–25	20	0	10	17.5–25	50	3	4
<i>Messor aegyptiacus</i>	16–25.5	17	0	46	19–28	22	0	28
<i>Monomorium salomonis</i>	12–25	25	2	46	18–28	250	36	29
<i>Crematogaster inermis</i>	12–25.5	35	12	37	11–28	220	56	45
<i>Pheidole pallidula</i>	12–24	25	22	28	11–27	62	6	5
<i>Monomorium pharaonis</i>	17.5–25	2	0	4	17.5–24	20	4	6
<i>Temnothorax arenarius</i>	–	–	–	–	20.5–21.5	6	6	0

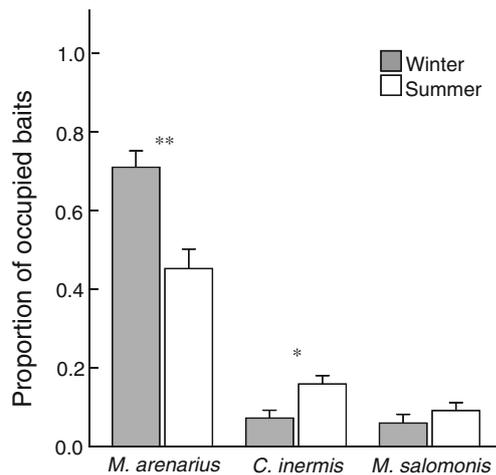
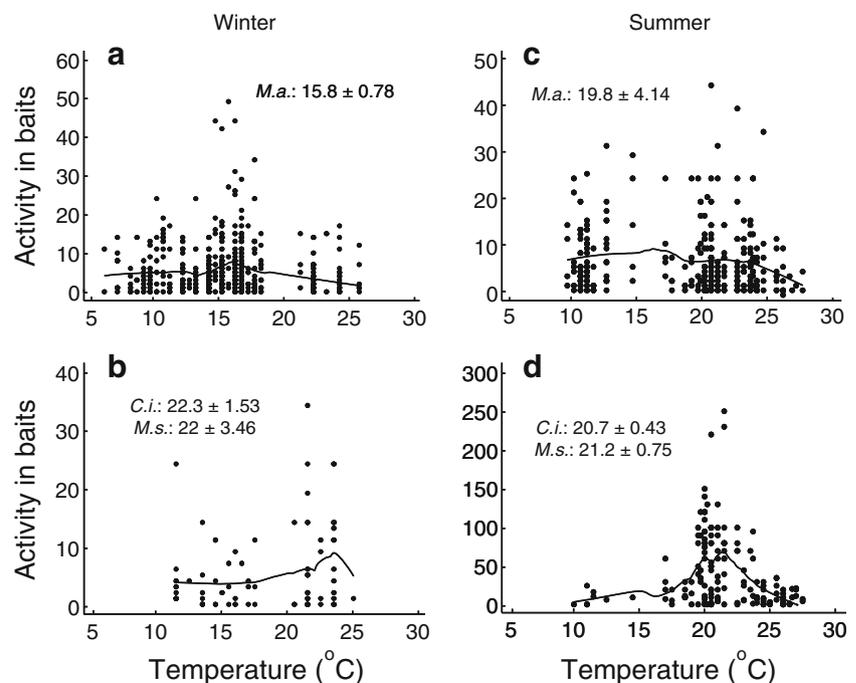


Fig. 1 Mean (+SE) proportion of baits occupied by the three study species, in relation to season. Significant differences between seasons within species are indicated above bars (* $P < 0.05$; ** $P < 0.01$; Tukey's test)

significantly decreased from winter to summer, that of *M. salomonis* did not change and that of *C. inermis* significantly increased (Fig. 1).

The temporal activity patterns of the three common species were also affected differently by season (two-way ANOVA: significant species by season interaction, $F_{2, 52} = 3.552$; $P = 0.036$). In winter, the numerically dominant *M. arenarius* was active at the baits at colder ground temperatures than the other two behaviorally dominant species ($F_{2, 22} = 15.857$; $P < 0.001$; Tukey's test, $P < 0.005$ (Fig. 2a, b)). In summer, there were no significant differences in the temporal activity of the three species ($F_{2, 30} = 0.895$, $P = 0.419$ (Fig. 2c, d)) (Table 1).

Fig. 2 The relationship between ground temperature and the foraging activity of the three study species in the baits, in relation to season. The numbers at the top of each figure are the ground temperatures (mean \pm SD) of thermal activity breadth (i.e., temperature at which 50% or more of the maximum number of foragers are active) for each species. (M.a. *Messor arenarius*, C.i. *Crematogaster inermis*, M.s. *Monomorium salomonis*). Lines represent LOWESS curves



In summer, *C. inermis* and *M. salomonis* showed aggressive behavior towards *M. arenarius* in 47% (38/81 encounters) and 46% (22/48 encounters) of the encounters between them, respectively. Moreover, there was a negative correlation between the number of foragers of either *C. inermis* or *M. salomonis* and the number of *M. arenarius* foragers at baits ($r_s = -0.506$; $P < 0.001$; $n = 215$ (Fig. 3a)). The logistic regression analysis showed that the presence of *M. arenarius* at baits was negatively related to the number of foragers of *C. inermis* and *M. salomonis* ($\chi^2 = 60.11$; $P < 0.001$; $n = 215$). There were only a few instances of encounters between foragers of *C. inermis* and *M. salomonis* in baits ($n = 139$ (Fig. 3b)). In addition, analysis of co-occurrence patterns of the three species at baits revealed that C_{obs} (value for the observed matrix) was significantly higher than C_{sim} (value for the simulated matrices; $P < 0.005$ for all combinations; Table 2), indicating that the species tend to avoid encounters with each other.

Significantly more seeds remained at baits in which *M. salomonis* and *C. inermis* were present, than at baits with *M. arenarius*, during summer nights (Kruskal–Wallis tests—*M. arenarius* vs. *C. inermis*, $\chi^2 = 39.7$; $P < 0.001$; $n = 150$; *M. arenarius* vs. *M. salomonis*, $\chi^2 = 25.08$; $P < 0.001$; $n = 134$; *C. inermis* vs. *M. salomonis*, $\chi^2 = 1.02$; $P = 0.31$; $n = 76$ (Fig. 4a)). In addition, significantly more seeds remained at baits in which *M. arenarius* was present during winter nights than during summer nights (Kruskal–Wallis test, $\chi^2 = 8.955$; $P < 0.005$; $n = 213$ (Fig. 4b)).

During summer days, the abundance and richness of seed-eating ant species was greater in baits that were occupied during the previous night by *M. salomonis* or *C.*

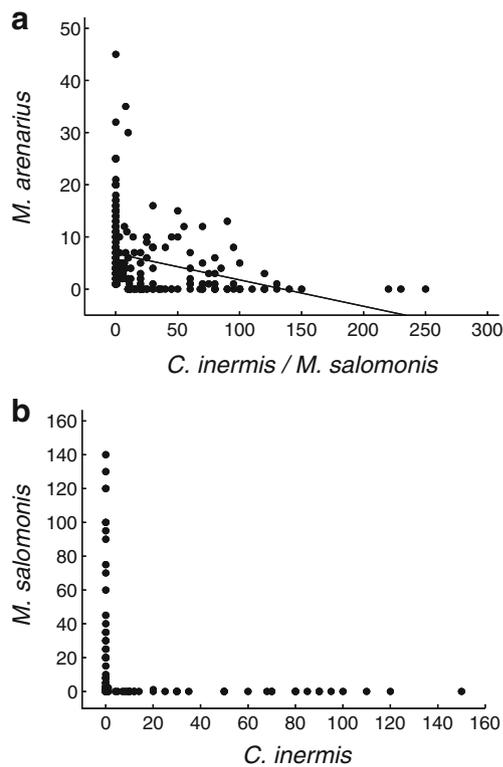


Fig. 3 Correlations between the number of foragers of the different study species at baits in the summer season. **a** Number of *M. arenarius* and *C. inermis* or *M. salomonis* foragers at baits. The line shows the correlation between *M. arenarius* and behaviorally dominant foragers in baits ($y = -0.047x + 6.49$, $r_s = -0.506$; $P < 0.001$). **b** Number of *C. inermis* and *M. salomonis* foragers at baits

inermis than by *M. arenarius* (abundance, $F_{2, 187} = 7.563$; $P = 0.001$ (Fig. 5a); richness, $F_{2, 187} = 5.867$; $P < 0.005$ (Fig. 5b)). Moreover, during summer days there were more instances of other seed-eating ant species occurring in baits that were occupied the previous night by *M. salomonis* or *C.*

Table 2 Co-occurrence patterns of the dominant ant species at food baits in the summer season

Species	Observed C score	Mean of simulated C score	<i>P</i> value
<i>Messor arenarius</i> vs. <i>Crematogaster inermis</i>	4,747	3,259	<0.005
<i>M. arenarius</i> vs. <i>Monomorium salomonis</i>	5,200	2,638	<0.001
<i>C. inermis</i> vs. <i>M. salomonis</i>	6,076	1,512	<0.001
<i>M. arenarius</i> vs. <i>C. inermis</i> vs. <i>M. salomonis</i>	5,341	2,896	<0.001

In a competitively structured assemblage, C score values should be significantly higher than expected by chance. Means of simulated C scores were produced following 5,000 randomizations of the observed presence–absence matrix. *P* values are for $C_{obs} > C_{sim}$

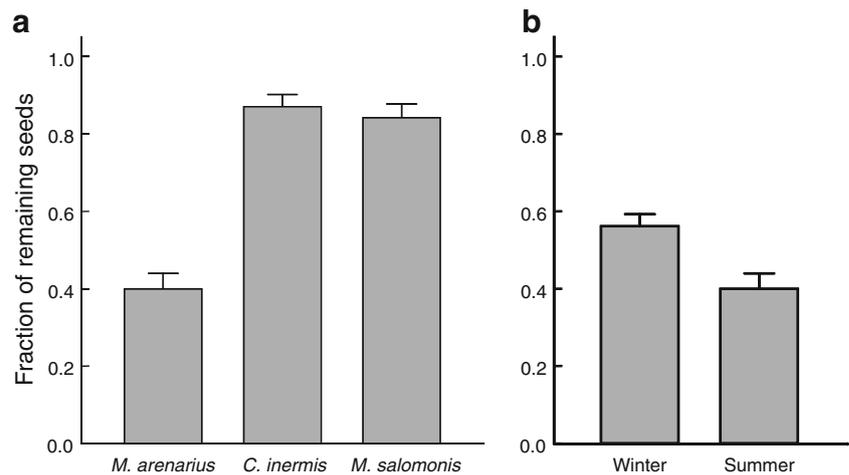
inermis than by *M. arenarius* foragers ($\chi^2 = 11.69$; $P < 0.005$; $n = 36$).

Discussion

Dominant ant species that differ in resource exploitation and manipulation could have varying impacts on the structure and organization of ant communities (Adler et al. 2007). In Mashabim Sands, this is demonstrated by the contrasting effects exerted by the numerically vs. behaviorally dominant species on the seed-eating ant species, whose foraging activity increased when the behaviorally dominant species (*C. inermis* and *M. salomonis*) were previously present at the baits compared to when the numerically dominant species (*M. arenarius*) was present (Fig. 5). While dominant ant species were mostly found to have a negative effect on the structure of ant communities (e.g., Andersen and Patel 1994; Morrison 2000; Sanders and Gordon 2000; Parr 2008), this study suggests the possible positive impact of behaviorally dominant species whose presence might facilitate the activity of other species when the numerically dominant species is present.

The negative effect of the numerically dominant species, *M. arenarius*, on the foraging activity of the subordinate species was possibly through resource depletion due to its high foraging efficiency. This is best exhibited by the lower number of seeds remaining on summer mornings at food baits that were occupied the previous night by *M. arenarius*, compared to baits that were occupied by the two behaviorally dominant species (Fig. 4), despite their greater ability to aggressively defend their food finds. The positive effect of the behaviorally dominant species could be attributed both to their low resource utilization and to their competitive interactions with *M. arenarius*. This is evident by the low co-occurrence of the three species at the baits, indicating that the species tend to avoid encounters with each other. Although this avoidance could be attributed to different habitat preferences of the ant species, this is most likely not the case here, as habitat structure was relatively homogeneous both within and among plots, and as most of the baits were seen occupied at different sampling days by more than a single species (Segev and Ziv, unpublished data). Additionally, the observed decrease in the number of baits occupied by *M. arenarius* during the summer compared to winter (Fig. 1), could result from the increased activity of the two behaviorally dominant species, which were found foraging at similar ground temperatures on summer nights (Fig. 2), during which they exhibited aggressive displays towards *M. arenarius* and monopolized the food resources (Fig. 3a). The behaviorally dominant species might thus provide an apparent facilitative effect, whereby food availability is maintained for other species. In food-limited

Fig. 4 Mean (+SE) fraction of seeds remaining in baits, in relation to the foraging activity of the study species. **a** *M. arenarius*, *C. inermis*, and *M. salomonis* foragers at baits in the summer season. **b** *M. arenarius* foragers at baits in winter vs. summer seasons. Mean fraction of seeds remaining was measured according to five equal fractions from 0 to 1



environments such as this arid region, this may also imply that an increase in food availability for different species could lead to an increase in species abundance and may enhance species diversity. Even though the nature of the experiment is observational and species occurrences at the baits and plots were not manipulated, we believe that our observations, which were replicated at the experimental baits over space and time, reflect how these two dominance

categories could affect this ant assemblage. However, interpretation of the results is limited to the foraging activity of species whose effect on ant species diversity could only be implied. In addition, it is important to note that our interpretation on the effect of the dominant species on the other seed-eating species is limited due to the low species richness in this ant assemblage.

The two behaviorally dominant species, *C. inermis* and *M. salomonis*, exhibited low encounter rates despite similar temporal activity patterns (Fig. 3b), which could suggest that they are highly antagonistic towards each other. Studies in other regions have shown that behaviorally dominant species may be distributed differently in space and/or time as a result of competition or different habitat preferences (e.g., on different islands or habitats, Cole 1983; Morrison 1996). In the present study, spatial partitioning was observed at a fine spatial scale among baits in the same plot, indicating that coexistence between ant species can be achieved even when resources are dispersed at a small spatial scale (e.g., Albrecht and Gotelli 2001; Stringer et al. 2007).

The increase in foraging activity of the seed-eating ant species during summer days in baits occupied the previous night by the behaviorally dominant species (Fig. 5) could also stem from a reduced ability of the behaviorally dominant species to defend their food resources when they are at lower numbers during the day. This notion is implied by the fact that most of their aggressive displays were exhibited at their *thermal activity breadth* at night (Figs 2 and 3). This also suggests that aggressive behavior might be affected not only by patch quantity and/or quality but also by surface temperature (Cerdá et al. 1997; Kaspari et al. 2000; Wittman et al. 2010), which could restrict the number of foragers in a patch. Similar evidence of increased aggressiveness with number of individuals in a group was exhibited in ants (Holway and Case 2001; Palmer 2004; Tanner 2006) as well as in other taxonomic groups, such as birds and mammals (Heinsohn 1997; Theuerkauf et al. 2009).

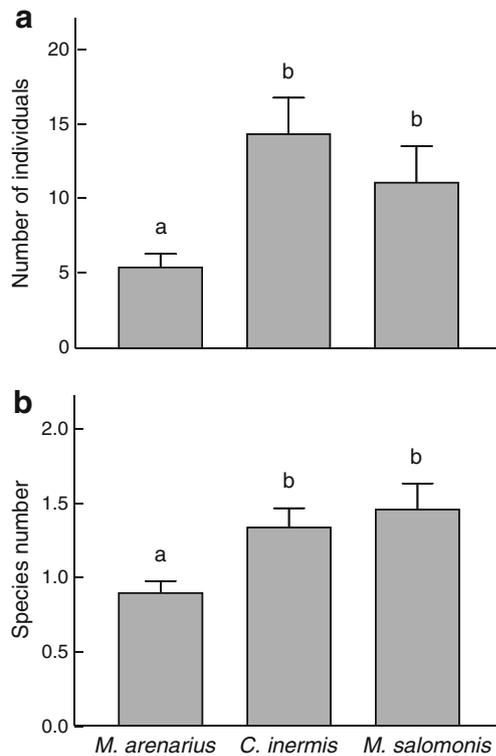


Fig. 5 **a** Mean (+SE) abundance and **b** mean (+SE) richness of the ant species in baits during summer days in relation to the presence of foragers of one of the study species in the same bait during summer nights. Different letters indicate statistically significant differences between species in Tukey's tests ($P < 0.05$)

In many ant assemblages, dominant species which occur at large proportion of baits are ranked high in their interspecific aggressive displays, such that numerical dominance is correlated with behavioral dominance (e.g., Andersen 1992; Human and Gordon 1996; Morrison 1996). However, in our study the numerically dominant species, *M. arenarius*, is ranked low in aggressive behavior, as suggested by the outcome of its interactions with the two behaviorally dominant species. Although *M. arenarius* is behaviorally subordinate, it possesses several morphological and behavioral characteristics that make it a numerically dominant species. These characteristics include high variability in body size, which allows foragers to carry seeds of variable sizes (see Kaspari 1996); a mixed foraging strategy of both individual and group foraging; and horizontally built nests (Kugler 1989; Steinberger et al. 1992). These traits enable efficient and rapid discovery and acquisition of food resources, especially when resource availability is low, as in Mashabim Sands. Moreover, during summer, when the three study species overlap in their foraging activity, *M. arenarius* was occasionally observed stealing seeds in the baits from one of the behaviorally dominant species, despite the risk of injury or even death. Our results are in accordance with those of Fellers (1987), who found an inverse correlation between exploitative and interference ability in a woodland ant assemblage (the “dominance-discovery trade off,” see also Davidson 1998; Parr and Gibb 2010).

Another characteristic of *M. arenarius* foragers, by which they were able to efficiently exploit the seed baits, is their ability to forage during winter nights, when no other species was observed outside the nest. This physiological cold-tolerance could allow *M. arenarius* to avoid interspecific competition and may be of great value in desert environments, where there is high variability between day and night temperatures. Several studies have found similar patterns of dominance-thermal tolerance trade-off, where the behaviorally dominants are less successful than the subordinate species in resource exploitation under extreme temperatures or are active within narrower ranges of temperature (e.g., Cerdá et al. 1998; Bestelmeyer 2000; Lessard et al. 2009).

The definition of dominance in our ant assemblage deserves a particular attention. For example, a widely used dominance hierarchy suggested by Savolainen and Vepsäläinen (1988) classifies ant species within a community according to their interference interactions into “territorials,” “encounterers” and “submissives.” Following this classification, the two behaviorally dominant species in our system correspond to the “encounter” species, which defend their nests and food sources, and not to the highest dominance category of “territorial” species, which defend also large foraging territories (e.g., Adams 1994; Andersen and Patel 1994). These “territorial” species, which are absent from our system but highly abundant in low- stress

environments (Andersen 2000), often exhibit both behavioral- and numerical-dominance characteristics (Andersen 1992; Cerdá et al. 1997). Davidson (1998) defined such species as “ecologically dominant” due to their important ecological effects on other species in the assemblage. According to this definition, the ant assemblage in Mashabim Sands is devoid of ecologically dominant species. However, as the three dominant species in our study exhibited important competitive effects on the other species in this community, we suggest that they might be considered ecologically dominants. This could be particularly true for *M. arenarius*, which occurred in large proportion of the food baits despite being subordinate in behavioral interactions. We therefore propose that being behaviorally dominant might not always be a requirement of ecologically dominant species.

In conclusion, our results demonstrate how two dominance types could have contrasting effects on the foraging activity of ant species in a community. Here, we show that dominant ant species do not necessarily have a negative effect on ant communities, especially when interacting with other dominants. Similar results were obtained recently by Arnan et al. (2011) who found that species of the highest level of dominance in the assemblage (corresponding to the “territorial” species of Savolainen and Vepsäläinen 1988) may promote the occurrence of subordinate species by suppressing the activity of the subordinate “encounter” species. Our results stress the importance of considering the effects of both behaviorally and numerically dominant species, and the interactions between them, when studying the mechanisms promoting coexistence in ecological communities. Further studies are required in order to learn whether the contrasting effects of the two types of dominant species found in this study are common to other assemblages with varying levels of resources and species richness.

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