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Consistent differences in foraging behavior in 2 sympatric harvester ant species may facilitate coexistence

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Abstract

The co-occurrence of 2 similar species depends on their ability to occupy different ecological niches. Here, we compared the consistency of different aspects of foraging behavior in 2 co-occurring harvester ant species (*Messor ebeninus* and *Messor arenarius*), under field conditions. The 2 species are active concomitantly and display a similar diet, but *M. arenarius* features smaller colonies, larger workers on average, and a broader range of foraging strategies than *M. ebeninus*. We characterized the flora in the 2 species' natural habitat, and detected a nesting preference by *M. arenarius* for more open, vegetation-free microhabitats than those preferred by *M. ebeninus*. Next, we tested the food preference of foraging colonies by presenting 3 non-native seed types. *Messor arenarius* was more selective in its food choice. Colonies were then offered 1 type of seeds over 3 days in different spatial arrangements from the nest entrance (e.g., a seed plate close to the nest entrance, a seed plate blocked by an obstacle, or 3 plates placed at increasing distances from the nest entrance). While both species were consistent in their foraging behavior, expressed as seed collection, under different treatments over time, *M. ebeninus* was more consistent than *M. arenarius*. These differences between the species may be explained by their different colony size, worker size, and range of foraging strategies, among other factors. We suggest that the differences in foraging, such as in food preference and behavioral consistency while foraging, could contribute to the co-occurrence of these 2 species in a similar habitat.

Key words: behavioral consistency, coexistence mechanisms, foraging, harvester ants, plant–ant interactions.

The coexistence of closely related species is intriguing, because large overlaps in foraging niches enhance the risk of competitive exclusion and local extinction (Connell 1961; MacArthur and Levins 1967; Amarasekare 2003). Co-occurring species must therefore not exceed a certain level of niche similarity in order to allow coexistence (Abrams 1983). Niche differentiation can take different forms, of which temporal partitioning is a common one (Kronfeld-Schor and Dayan 2003). For instance, 2 gerbil species foraging in desert sand dunes for the same seeds are not active simultaneously: one species *Gerbillus pyramidum* is active in the early night hours while the other *Gerbillus allenbyi* in the later part of the night (Kotler et al. 1993; Ziv et al. 1993). Spatial niche partitioning presents another mechanism of species coexistence. For example, in desert rodents, large granivorous rodents with strong hind legs prefer open habitats with sparse vegetation, while smaller rodents walking equally on all 4 legs occur more under bushes (Kotler and Brown 1988).

Coexisting species may differ too in their preferred diet, reflected, for example, in different teeth length (Dayan et al. 1989, 1990). They can also differ in their diet breadth, being opportunistic or selective in their prey choice (Bonesi and Macdonald 2004).

Finally, some coexisting species differ in their trade-off balance point between exploration and exploitation: some are better at detecting food, while others are better at exploiting it (Vance 1984; Ziv et al. 1993; Avgar et al. 2008; Mehlhorn et al. 2015).

Ants are central-place foragers that retrieve food to their nests for consumption, to feed kin, or for storage. Two common questions of central-place foraging are those of how an organism that possesses a nest/burrow should most effectively choose among food patches and types, and how it should handle items of various sizes (Holder-Bailey and Polis 1987; Wetterer 1989). Ant species often coexist in the same habitat, and all of the above coexistence mechanisms exist in ants. Partitioning in space is mostly related to the maintenance of territories, which depends on available food and the presence of competing colonies (Solida et al. 2010, 2011a; Czechowski et al. 2013; Houadria et al. 2015). Co-occurring ants also demonstrate temporal-partitioning, with distinct seasonal and daily peaks of foraging, enhancing coexistence (Andersen 1983; Cerdá et al. 1998; Albrecht and Gotelli 2001). The exploration–exploitation trade-off (also known as the discovery-dominance trade-off) is common in ant communities, based on the number of foragers: species with either more or fewer foragers specialize in exploitation and exploration, respectively (Davidson 1998; Pierce-Duvet et al. 2011).

Models of optimal diet choice predict that animals should be more selective of specific food types in rich habitats but more selective of specific patches in poorer habitats (MacArthur and Pianka 1966; Kotler and Mitchell 1995). Other models predict that animals should start by exploiting patches as specialists, but should then shift to a more opportunistic diet, and should do so faster, the longer they stay in a single patch. Patch residency time is expected to correlate with the time required to reach the patch (Heller 1980; Brown 1988; Barrette et al. 2010). Opportunistic and selective foragers are characterized by different consistency levels in their diet choice. Such differences in consistency levels of foraging-related behaviors are important for understanding how species survive, reproduce, and coexist in their natural environment. Furthermore, behavioral consistency of an entire colony has been shown for different behaviors (e.g., Pinter-Wollman et al. 2012; Scharf et al. 2012). Such consistency—the behavioral variation explained by inter-individual (or colony) differences (Bell et al. 2009)—is important due to several reasons, including its link to heritability levels (Boake 1989) and in being a first step prior to the determination of personality (Bell et al. 2009).

Three key traits of ants often affect foraging performance: (1) worker body size is positively related to the maximal distance traveled (termed "the size–distance relationship"; McIver and Loomis 1993; Wright et al. 2000), probably because travel costs for larger workers are lower. Larger workers also collect larger food items (Davidson 1977a; Retana and Cerdá 1994; Kaspari 1996); (2) colony size is positively correlated with worker recruitment ability and territorial domination (Beckers et al. 1989; Gordon and Kulig 1996), and affects the foraging strategy applied by the colony, from individual to mass recruitment (Beckers et al. 1989; Dornhaus and Powell 2010, but see Bengston and Dornhaus 2013); and (3) the foraging strategy can determine the location of each species on the exploration–exploitation trade-off scale. Generally, group-foraging species are more efficient in exploiting food patches, while individual foragers are better at detecting new patches (Davidson 1977b; Avgar et al. 2008).

We studied here the microhabitat preference, diet preference and breadth, and foraging behavior consistency of 2 congeneric co-occurring seed harvester ant species: *Messor arenarius* and *Messor ebeninus*. Regarding microhabitat preference, another study showed significant differences in microhabitat attributes of nesting sites between 2 different *Messor* ant species. Among other attributes, they differ in the presence of particular plant species (Solida et al. 2011b). Generally, harvester ants and plants exist in a state of mutualism (Hölldobler and Wilson 1990), and vegetation is about 5 times denser close to harvester ant colonies than at adjacent, ant-free, sites (Rissing 1986). Specifically, distinct separate preferences for particular vegetation would contribute to the 2 species' ability to coexist. We expected that, due to its more arid climate distribution in general, *M. arenarius* would be found further away from vegetation.

Furthermore, we expected a difference in seed preference (diet breadth) and in the consistency of foraging behavior that could also contribute to the 2 species' coexistence. Although both species are polymorphic, *M. arenarius*, featuring larger body size on average, but smaller colony size, and foraging either individually or in small groups, was expected to be more selective of specific seeds but more opportunistic in its preferred food patches. *Messor ebeninus*, a group forager, was expected to be more opportunistic than *M. arenarius* in collecting seeds but more selective in food patches. Selecting specific high-quality patches would be more important for *M. ebeninus*, which forages in large groups. Selecting high-quality seeds would be more important for the mostly individual foraging *M. arenarius*, because of its lower tendency to recruit and because depletion of the patch might be more challenging for this species.

Materials and Methods

We first characterized the habitat in which the 2 *Messor* species co-occur and examined whether they display distinct nesting preferences for vegetation cover. We then examined the seed preference of these 2 species, from among 3 non-local seed types. Finally, we examined inter-colony differences and intra-colony consistency in foraging behavior under 3 different settings for 3 days, and tested for associations between colony behavior in each of the 3 different settings.

Studied ants

We used 2 co-occurring *Messor* species (subfamily: Myrmicinae; tribe: Pheidolini), *M. arenarius* and *M. ebeninus*, as our experimental animals. *Messor arenarius* is heavier and larger than *M. ebeninus* (an average of 42 mg and 3.13 mm vs. 7 mg and 1.92 mm; body mass and head width, respectively; Segev et al. 2014), but both are polymorphic. *Messor arenarius* is distributed mainly in deserts of the Middle East and North Africa, while *M. ebeninus* occurs in Europe, West Asia, and North Africa (Collingwood 1985; Kugler 1988; Vonshak and Ionescu-Hirsh 2009). *Messor arenarius* is numerically dominant over other seed-harvester species, including *M. ebeninus* (according to findings from bait-trapping; Segev and Ziv 2012). Finally, *M. ebeninus* colonies comprise ~100,000 individuals, while *M. arenarius* colonies only comprise up to 5,000 individuals (Steinberger et al. 1991). Both species forage on plant seeds, other plant material, and occasionally also on dead invertebrates, but the average weight per worker carried back to the nest by *M. arenarius* is greater than that carried by *M. ebeninus* (Steinberger et al. 1992; Plowes et al. 2013; Segev et al. 2014). The 2 species collect seeds of similar sizes and co-occur in the same habitats in Israel (Steinberger et al. 1991; Segev 2010; this study).

Furthermore, the 2 species differ in their common foraging strategy. *Messor ebeninus* is mostly a trunk-trail or group forager (Kunin 1994; Avgar et al. 2008), although group foragers are also able to forage individually (Bernstein 1975). *Messor arenarius* is more frequently an individual forager but can also be a group forager, with considerable differences among *M. arenarius* populations (mostly individual forager: Warburg 1996, 2000; Avgar et al. 2008; mostly group forager: Wilby and Shachak 2000; mixed: Steinberger et al. 1991, 1992; Segev and Ziv 2012). Some harvester ants show a flexible foraging strategy based on seed density and distribution, which may explain this mixed evidence (Pol et al. 2015).

Study site

Tel Baruch coastal sand dunes (32.1283 N, 34.7867 E; ~20 m above sea level) are adjacent to the Mediterranean coast in north-west Tel Aviv (~250 m). The area is about 1.5 × 0.5 km (length × width), and receives ~550 mm mean annual rainfall, of which 80% occurs between November and February. Mean temperatures in August and January are 25.4 °C and 12.4 °C, respectively (BioGIS 2016). The dunes are roughly divided into stabilized (southern part) and semi-stabilized areas (northern part). The area is surrounded by city neighborhoods, and is frequently disturbed by human activity, similar to a city park, although the flora is primarily wild and the area is not irrigated.

Plant cover and sampling

We characterized the flora of Tel Baruch by sampling the plants and determining plant cover (Abramsky et al. 1985). Characterizing the habitat is important as a background for field studies in general, and for the study of seed-harvesting ants in particular, as they rely on vegetation for foraging. Four grids were established, each marked with 40 stations in 4 rows, at 5 m intervals between stations and rows (Figure 1). Plant cover and sampling were conducted in winter (February–March) and spring (May) of 2 consecutive years, 2014–2015. Grids were divided between the stabilized and semi-stabilized sand dunes. For each grid, 12 stations were randomly selected. Plant cover was determined using the line-intercept method (Canfield 1941) and was conducted as follows: from each of the 12 chosen stations, we deployed a 10 m measuring tape in a random direction. Plant species and length cover (cm) of both perennial and annual plants under the measuring tape were documented. Plant sampling was conducted as follows: the first, second, and third perennial plant closest to the focal stations were documented (plant species, length, width, and distance from the station). The nearest plant neighbor (Clark and Evans 1954) to the first closest perennial plant was also documented, resulting in 4 perennial individual plants sampled per station. Finally, we documented the nearest ant colony to the station and the nearest perennial plant to the ant colony.

Field experiments

All experiments were performed between March and June of 2014–2015. The seed preference test for *M. ebeninus*, as the only exception, was performed in November 2015. Although there is some evidence of seasonal effects on natural seed preferences, depending on their natural occurrence (Crist and MacMahon 1992), we did not expect a seasonal difference to exist in non-natural seed preference, as such seeds do not occur in the ants' natural habitat. The 2 field experiments were performed during noon hours, when typical high activity can be observed for the 2 species. Nevertheless, we relied on a previous report that shows the 2 species are active simultaneously, under similar temperatures, and show the same seasonal activity changes (Steinberger et al. 1992). During both experiments, all colonies were circumscribed by a tracking trail, to trace and exclude foraging by other animals, such as crows and beetles (see the Supplementary Material for a detailed explanation on the construction of the tracking trail). Seeds (2 g) were weighed in the laboratory before and after the experiment, in order to calculate foraging efficiency (mass collected within a given time period). Air and ground temperatures and relative humidity were measured at the beginning and end of each work day, using Sh-101 Digital Thermo-Hygrometer, by ISOLAB (see Supplementary Table S1 in the Supplementary Material). No special permits were required for any of the experiments.

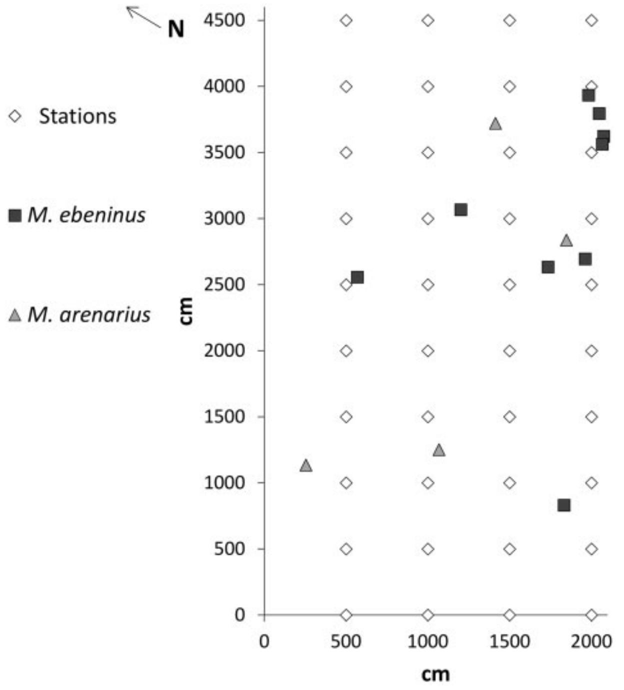

Figure 1. One of the 4 grids created at the study site, presenting the stations established (diamonds) as base for plant sampling and plant cover. *Messor arenarius* (triangles) and *M. ebeninus* (squares) co-occur and overlap in their habitat.

Experiment 1: seed preference

We examined the preference of the 2 ant species for 3 seed types, relatively similar in size, provided in 2 different spatial arrangements (treatments), by documenting the amount collected of each seed type, with all 3 being offered simultaneously. We used non-native seeds: millet, sesame, and rice (see Supplementary Material, Supplementary Table S2, for their nutritional value, and Supplementary Figure S1 for a photo showing both species foraging on millet seeds). Non-native seeds enable standardization of the nutritional value of each seed type and ensure year-round experimental access to them (Davidson 1978; Avgar et al. 2008). Twelve and 15 colonies of *M. arenarius* and *M. ebeninus*, respectively, were tested. Five-to-eight colonies received one treatment per day, in a randomized order of treatments, over 2 weeks (each colony was tested twice with a 24-h interval). The tests were conducted for 2 h for *M. arenarius* and 40 min for *M. ebeninus*. The experiment was shorter for *M. ebeninus*, because of its faster depletion of the food patch. Individual foragers, or weak group foragers, like *M. arenarius*, typically take longer than strict group foragers to search out and collect seeds (Davidson 1977b). We presented the ants with the 3 choices of

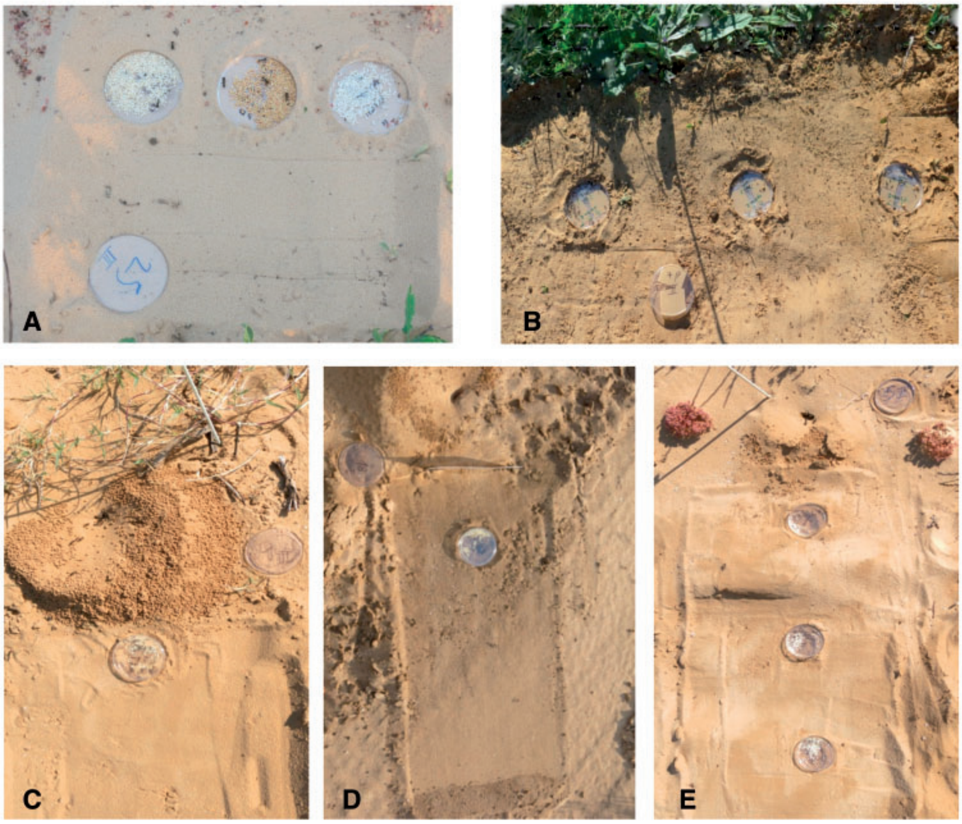

Figure 2. The spatial arrangements of the seed plates in the 2 field experiments. *Seed preference:* (**A**) clustered patches, (**B**) scattered patches. *Consistency of foraging behavior:* (**C**) 30 cm, (**D**) obstacle, and (**E**) distances (30, 60, and 90 cm). Nest entrance is visible in C–E (upper part of the photo). An additional empty plate presents the nest ID number.

seeds (millet, sesame, and rice) in 9-cm Petri dishes, similar to previous studies on harvester ants (Davidson 1977b; Kunin 1994; Avgar et al. 2008). We employed the 2 following treatments, one treatment per day: (1) "Clustered patches": 3 plates were placed horizontally, on the tracking trail, 30 cm from the entrance to the nest and 3 cm between plates (Figure 2A). (2) "Scattered patches": 3 plates were placed horizontally, on the tracking trail, 30 cm from the entrance to the nest and 30 cm between plates (Figure 2B). All treatments took place on one tracking trail that was cleared and renewed between treatments.

Experiment 2: consistency of foraging behavior

The aim here was to determine whether colonies of the 2 ant species exhibit consistency in foraging behavior, expressed as the amount of collected seeds, over time and in different foraging contexts (treatments). We used millet seeds for this experiment, as they had been found to be most preferred by *M. arenarius*, while *M. ebeninus* had shown no preference (see the "Results" section). Twenty-eight and 29 colonies of *M. arenarius* and *M. ebeninus*, respectively, were tested for 2 months. Four-to-eight colonies were tested under 3 different treatments per day for 2 consecutive days (days 1 and 2), followed by 1 day of rest and then another day of testing (day 3). All treatments were conducted for 50 min for *M. arenarius* and 20 min for *M. ebeninus*, with an interval of 20 min between treatments. As said, the experiment was shorter for *M. ebeninus* because of its faster depletion of the food patch. Treatments were given in a random order: (1) "30 cm": a plate with millet seeds was placed on the tracking trail, 30 cm from the entrance to the nest (Figure 2C); (2) "obstacle": a plate with millet seeds was placed on the tracking trail, 30 cm from the entrance to the nest. Next, a 16 × 8 cm white plastic obstacle was placed between nest entrance and plate, 15 cm from the entrance. The purpose was to increase the energetic cost of searching by increasing the distance the workers had to cross (Figure 2D); and (3) "distances": 3 plates with millet seeds were each placed on the tracking trail, 30, 60, and 90 cm from the entrance to the nest (Figure 2E). For comparison with the previous 2 treatments, we approached this treatment in terms of number of plates on site and thus divided it into 3 sub-treatments. In total, we applied 5 treatments in this particular experiment. All treatments took place on one tracking trail that was cleared and renewed between treatments.

Statistical analyses

We analyzed plant cover and plant sampling separately.

Plant cover

We used a repeated-measures ANOVA to analyze plant cover: perennial and annual species (length in centimeter, up to 1,000 cm) were used as response variables (measured simultaneously using the measuring tape), with year and season as explanatory variables. Perennial and annual covers were square-root transformed due to their deviation from normal distribution.

Plant sampling

We analyzed the 3 most common perennial plant species out of all plant species documented, with each of the 3 comprising more than

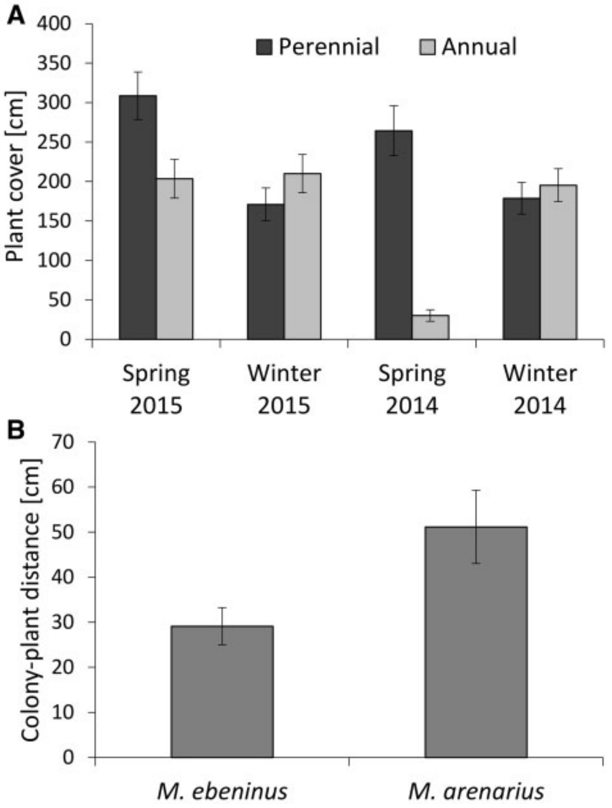

Figure 3. (**A**) Perennial and annual plant cover (of 1,000 cm) at the study site in spring and winter of 2014 and 2015 (mean ± 1 SE). (**B**) The distance (cm) of *M. ebeninus* and *M. arenarius* colonies to the nearest perennial plant (mean ± 1 SE).

10% of the total vegetation. We used 2 χ^2 tests to compare the abundance of the 3 plant species between seasons and years.

Ant colony-perennial plant distance

We compared the distance of the closest perennial plant to each ant colony using 3-way ANOVA, with ant species, season, and year as the explanatory variables and distance as the response variable. In this analysis all null values were removed (if a colony was not found up to a radius of 5 m from the sampled station). Distance to the perennial plant closest to the ant colony was $\log_{10}$-transformed.

Experiment 1: seed preference

We asked 3 questions: (1) *Seed preference:* Do the 2 studied species reveal a preference for specific seeds and does this preference differ between the species? We performed a repeated-measures ANOVA (seed types were presented to colonies simultaneously, for choice) for each treatment separately (clustered and scattered patches), and used species as an explanatory variable and the proportions of collected seeds as response variables. Proportions of seeds collected were arcsine-transformed. (2) *Difference between spatial treatments:* Is there an effect of treatment (clustered vs. scattered patches) on this preference? We calculated a preference index (Shannon–Wiener's index) of the amount collected of each seed type. Low values indicate a strong preference for specific seeds (selectivity) while high values indicate a weak preference (opportunism); this preference index was used also in the seed preference consistency analysis (see below). We used repeated-measures ANOVA, with species as the explanatory variable and the preference indices of the 2 treatments (clustered vs. scattered patches) as response variables. (3) *Seed preference consistency:* Are colonies within each species consistent in their preference between treatments? We used a Pearson correlation to test for a link between the preference indices of the 2 treatments. A separate correlation analysis was conducted for each species. If colonies are consistent in their degree of selectivity, we would expect a positive correlation in their preference index across the 2 treatments.

Experiment 2: consistency of foraging behavior

We analyzed behavioral consistency of all treatments between days. For this purpose, we used intra-class correlations (hereafter ICC): (1) to test for correlations between the quantity of collected seeds ($\log_{10}$-transformed) per treatment and separately for each species, across all days (1, 2, and 3), in order to test for general consistency level; and (2) consistency between the first and last days (1 and 3), in order to test whether consistency declines faster in one species than the other. High ICC values indicate high behavioral consistency. All data were analyzed using Systat v. 13 and Statistica v. 7.

Results

Plant cover and sampling analysis

Plant cover and sampling were conducted in 2 consecutive years (2014–2015), during the seasons with highest vegetation (winter and spring) each year. Sixteen perennial species were identified (first, nearest neighbor to first, second and third closest to focal stations; $N = 758$). A total of 13 annual plants were identified to species level, 3 to genus level, and 1 to family level. Eighteen percent of annual plants were unidentified and classified as "non-perennial plants". The 3 most common perennial species were *Sporobolus pungens* (28.3% of the total perennial species), *Centaurea procurrens* (20.3%), and *Echium angustifolium* (12.3%). See Supplementary Table S3 in the Supplementary Material for a list of typical perennial species identified.

Colonies belonging to 5 ant species were identified by direct observations in all seasons and grids: *M. arenarius* (33.8% of total ant colonies), *Cataglyphis niger* (33.1%), *M. ebeninus* (25.6%), *Cataglyphis livida*, and *Camponotus fellah* (the latter 2 comprising less than 8%; total $N = 160$ colonies).

Plant cover: The 3-way interaction plant type × year × season had a significant effect on plant cover ($F_{1,187} = 8.85$, $P = 0.003$). Perennial cover was higher and lower in spring and winter, respectively, in both years. The annual cover showed a different pattern, with similar levels overall, except for spring 2014, which was much lower (Figure 3A). The 2-way interactions were also both significant (plant type × year: $F_{1,187} = 10.83$, $P = 0.001$; plant type × season: $F_{1,187} = 57.54$, $P < 0.001$). Lastly, plant type and year were significant, as main effects ($F_{1,187} = 32.99$, $P < 0.001$; $F_{1,187} = 17.21$, $P < 0.001$, respectively), but season was not ($F_{1,187} = 0.23$, $P = 0.63$). Based on the Israeli meteorological site (http://www.ims.gov.il), precipitation in the rainy season of 2015 was higher than average (106%), whereas in 2014 it was lower than average (62%), which may explain the lower annual plant cover in spring 2014 (Figure 3A).

Plant sampling: There was no difference among the 3 most abundant perennial plant species between 2014 and 2015 ($\chi^2 = 0.32$, df = 2, $P = 0.85$). However, there was a marginally non-significant difference between seasons: in winter, the abundance of *S. pungens*

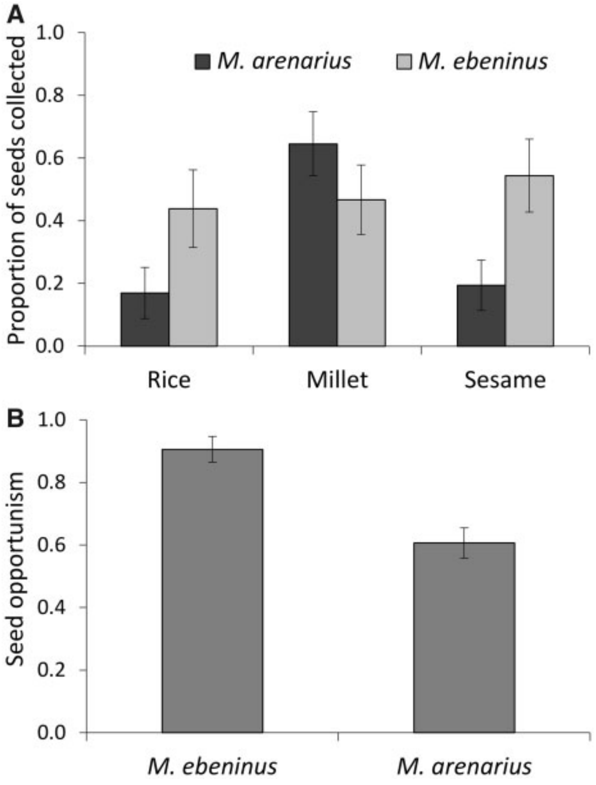

Figure 4. (**A**) The proportions of seeds collected by *M. ebeninus* and *M. arenarius* when offered millet, sesame, and rice (treatment 1; clustered patches). (**B**) Seed opportunism of both ant species. Lower and higher values indicate higher selectivity and higher opportunism, respectively (mean ± 1 SE).

was proportionally higher than in spring ($\chi^2 = 5.45$, df = 2, $P = 0.066$; Supplementary Table S4 in the Supplementary Material).

Ant colony-perennial plant distance: Distance of the ant colony to the nearest perennial plant differed according to the nearest *Messor* ant colony (plants were found closer to *M. ebeninus* than to *M. arenarius*: $F_{1,67} = 4.10$, $P = 0.047$; Figure 3B), while both year and season were not significant ($F_{1,67} = 0.23$, $P = 0.63$; $F_{1,67} = 0.08$, $P = 0.77$, respectively). The 3-way interaction and all 2-way interactions were not significant ($P > 0.07$ for all) and were removed.

Experiment 1: seed preference

Seed preference: For treatment 1 (clustered patches), seed preference differed between the species, indicated by the significant species × seed interaction ($F_{2,50} = 7.09$, $P = 0.002$; Figure 4A). While *M. arenarius* strongly preferred millet, *M. ebeninus* collected similar proportions of the 3 seed types. Seed type as a main effect was also significant, with a general preference for millet ($F_{2,50} = 4.29$, $P = 0.019$), but the 2 species did not differ in the amount of collected seeds ($F_{1,25} = 1.68$, $P = 0.21$). For treatment 2 (scattered patches), the results were similar, with a significant species × seed interaction ($F_{2,50} = 17.08$, $P < 0.001$), significant seed type as a main effect ($F_{2,50} = 17.51$, $P < 0.001$) and a non-significant difference between the 2 species as a main effect ($F_{1,25} = 0.53$, $P = 0.47$); see Supplementary Figure S2 in the Supplementary Material.

Difference between spatial treatments: The 2 treatments were compared using the calculated preference index. There was no difference between the 2 treatments (treatment: $F_{1,24} = 0.89$, $P = 0.35$) but only between species ($F_{1,24} = 19.96$, $P < 0.001$), with *M. arenarius* being more selective (Figure 4B). The 2-way interaction (treatment × species) was not significant and was removed ($F_{1,24} = 0.01$, $P = 0.92$).

Seed preference consistency: Using the preference indices, *M. ebeninus* was found to be consistent between treatments ($r = 0.627$, $P = 0.017$) while *M. arenarius* was not ($r = -0.481$, $P = 0.134$). See Supplementary Figure S3 in the Supplementary Material for a correlation graph, comparing both species.

In conclusion, *M. arenarius* was more selective in seed preference than *M. ebeninus* and preferred millet seeds. However, *M. ebeninus* was more consistent between treatments than *M. arenarius*.

Experiment 2: consistency of foraging behavior

Regarding the foraging pattern by seeds collected in each treatment, colonies of *M. ebeninus* were consistent over a longer time period than *M. arenarius*, with the former being significantly consistent in more treatments according to the ICC. Specifically, comparing days 1–3 (a 4-day interval), *M. arenarius* was never consistent, while *M. ebeninus* showed consistency in 2 of the 5 treatments. Comparing all days (1–2–3 days), *M. ebeninus* was consistent in all 5 treatments but *M. arenarius* in only 3 of the 5 treatments (Table 1). This suggests that *M. ebeninus* collected similar amounts of seeds between days and across treatments, and was thus more consistent in its foraging behavior than *M. arenarius*.

Discussion

In order for co-occurring species to coexist, they need to differ in some axes of their niche (Kotler and Brown 1988). We examined several aspects of foraging behavior and vegetation preference of 2 congeneric and co-occurring harvester ant species. First, when tested for consistency in patch exploitation under different foraging contexts, *M. ebeninus* was consistent for longer and under more treatments than *M. arenarius*. Furthermore, *M. ebeninus* showed consistency between treatments in seed preference: colonies that were selective in one situation were also selective in others, and vice versa for non-selective colonies. However, *M. arenarius* was more selective than *M. ebeninus* in its preference for a specific seed type. In short, *M. arenarius* was selective in regard to the food type chosen and *M. ebeninus* was selective in regard to the patch in which they chose to forage. Finally, *M. ebeninus* colonies were located closer to vegetation than those of *M. arenarius*.

We found some segregation in space in these species, which is a common mechanism of species coexistence. Colonies of *M. ebeninus* position themselves closer to perennial plants than *M. arenarius*, although their foraging territories also overlap (Figure 1). This segregation, although at a fine scale, is perhaps due to *M. arenarius* originating from desert habitats with sparse vegetation, compared with the more Mediterranean distribution of *M. ebeninus*. In a comparative example, a larger desert gerbil species prefers open habitats while a smaller species is found in bushier ones, perhaps due to different levels of predation risk or to different effects of seed distribution by wind on the 2 gerbil species (Brown et al. 1988; Ben-Natan et al. 2004). While preference of the larger ant species for the open habitat and of the smaller one for the bushier habitat seems to be similar to that of the desert gerbils, the mechanism behind this remains to be tested in the *Messor* species. Note that the between-species difference in the mean distance of colonies to perennial plants, although significant, is about 20 cm. The importance of such a short distance for the colonies in their natural habitat remains to be explored.

Table 1. Consistency of seed collection, under 5 treatments, was measured using intra-class correlation (ICC) through days 1–2–3 and between days 1 and 3, for *M. ebeninus* (A) and *M. arenarius* (B)

Treatments/days	1–2–3			1–3		
	ICC	95% CI	*P*	ICC	95% CI	*P*
(A) *M. ebeninus*						
30 cm	0.594	0.367–0.779	**<0.001**	0.606	0.276–0.808	**0.001**
Obstacle	0.307	0.066–0.561	**0.005**	0.286	−0.107–0.601	0.074
30 distance	0.566	0.342–0.754	**<0.001**	0.425	0.053–0.694	**0.014**
60 distance	0.478	0.241–0.694	**<0.001**	0.210	−0.186–0.547	0.147
90 distance	0.319	0.078–0.572	**0.004**	0.238	−0.157–0.567	0.116
(B) *M. arenarius*						
30 cm	0.460	0.211–0.689	**<0.001**	0.184	−0.211–0.528	0.178
Obstacle	0.429	0.178–0.666	**<0.001**	0.199	−0.197–0.539	0.160
30 distance	0.282	0.039–0.546	**0.011**	0.197	−0.199–0.538	0.162
60 distance	−0.016	−0.208–0.259	0.536	0.060	−0.336–0.438	0.385
90 distance	−0.141	−0.299–0.119	0.873	−0.024	−0.424–0.384	0.544

Note: Significant results appear in bold.

Temperature affects foraging performance and preferences of ants (Byron et al. 1980; Traniello et al. 1984). Different thermal performance curves of 2 co-occurring species may enhance resource partitioning and improve the likelihood of their coexistence (Persson 1986). The studied *Messor* species forage mainly simultaneously, under similar temperatures (Steinberger et al. 1992). Therefore, mechanisms underlying competition between these 2 studied species unrelated to temperature should be further studied.

Another putative coexistence mechanism is reflected in the opportunism–selectivity axis, which differs between the 2 *Messor* species in relation to diet and patch. *Messor arenarius* was more diet selective than *M. ebeninus*. The former species may have preferred the millet seeds because they contain a better trade-off between carbohydrates and proteins than rice (81% and 14% in millet and 91% and 8% in rice, respectively; Supplementary Table S3). Differences in diet breadth are a suggested mechanism of species coexistence also in other multi-species systems, such as woodrats and mink (Dial 1988; Bonesi and Macdonald 2004). That said, it remains to be determined whether similar differences between the 2 ant species exist concerning the natural seeds available in their shared habitat.

Messor arenarius, the larger species, which forages more individually than *M. ebeninus*, was selective in its seed preference but opportunistic in its patch choice (i.e., less consistent between days). Although there is some evidence that travel costs are relatively low in general, for harvester ants (Baroni-Urbani and Nielsen 1990; Plowes et al. 2013), it is plausible that the energetic cost of travel for the larger ant species is lower. This result corresponds to studies showing that larger workers travel longer distances from the nest than smaller ones (e.g., McIver and Loomis 1993). *Messor arenarius* is more selective perhaps also because selecting specific seeds has a higher temporal cost for the group forager than for the more individually foraging ant. *Messor ebeninus* was more consistent in its patch exploitation, probably due to its stronger group-oriented foraging strategy that, combined with its large colony size, enabled the recruitment of many workers to thoroughly exploit and detect a patch. Because patches differ more strongly in their value for *M. ebeninus*, patch exploitation was more consistent for this species. Generally, larger species discover food patches faster than smaller ones but are less efficient while foraging (Brown 1989), which is probably also the case here.

There are several other possible explanations for the higher patch exploitation consistency of *M. ebeninus*. First, higher consistency could be linked to colony size, with the larger number of foragers increasing colony consistency through specializing on specific food patches. Large colony size often enhances worker specialization and probably increases inter-colony differences (Holbrook et al. 2011). A larger colony could also mean more intra-colony interactions, leading to more stable colony behavior and larger inter-colony differences. Second, *M. arenarius* is more diverse in its foraging strategies than *M. ebeninus*, perhaps contributing to its lower consistency in patch exploitation.

Animals are expected to be less diet-selective when inter-patch distances increase, because the distance to or the likelihood of detecting the most preferred food type diminishes (Levey et al. 1984; Stephens and Krebs 1986, ch. 2; Dumont et al. 2002). Our present findings, however, do not support this expectation, because the inter-patch distance had no effect on seed selectivity of both *Messor* species. Moreover, in a similar seed preference test for *M. ebeninus*, this species showed no preference for a specific seed type, even when a density factor was considered (rare vs. common; Kunin 1994). This is not to say that harvester ant selectivity is entirely unaffected by foraging distance: harvester ants sometimes become more selective with foraging distance [see Detrain et al. (2000) and references therein for increased selectivity or no change]. However, although foraging distances may play a role in the foraging patterns of harvester ants, we have shown here that the species-specific differences in foraging strategies can be detected even in short foraging bouts. Finally, it has been suggested for harvester ants that travel distance and energetic cost are not the main consideration of foraging workers, but rather the temporal cost (Fewell 1988; Weier and Feener 1995).

In summary, different mechanisms have been suggested to explain how 2 similar harvester ant species coexist, such as diet partitioning in respect to seed type and size, or different foraging strategies (Davidson 1977a; Cerdá and Retana 1994; Solida et al. 2011a). In our case, we suggest that differences in colony size, worker size, and the broader range of foraging strategies have led to different microhabitat preferences and especially to different levels of selectivity regarding seed types and patches. In other words, coexistence may be supported by a difference in the level of behavioral consistency of the 2 species. The findings from such studies of behavioral consistency can contribute to improving our understanding of the mechanisms of species coexistence.

Author Contributions

M.S. and A.S. conceived and designed the experiments. I.S. and J.N.P. helped in designing the experiment. M.S., I.R., and T.L. performed the experiments. M.S. and I.S. analyzed the data. M.S., A.S., and I.S. wrote the manuscript. J.N.P. provided editorial advice.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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