



Efficiency of foraging behavior in the ant genus *Messor* (Hymenoptera: Formicidae: Myrmicinae) in response to food distribution

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Abstract. Harvester ants are known to be species that collect seeds of plants and store them in underground chambers. Workers forage solitarily or in groups, and the intensity of their foraging depends, among other things, on the rate of food intake. To evaluate the efficiency of foraging in response to food distribution, we studied the foraging rate on different distributions of seeds in three species of the genus *Messor*, *M. barbarus* (Linnaeus, 1767), *M. maroccanus* Santschi, 1927 and *M. sanctus* Emery, 1921. Foraging rates were higher on more clumped seed distributions in all studied colonies. The number of foragers did not influence the foraging behavior of these colonies in response to seed distribution. Monitoring the foraging rate over time revealed that it remains stable for all three species, except for the initial and final stages of bait consumption. Additionally, *M. maroccanus* collected seeds from several sources simultaneously, whereas the other two species collected seeds from one resource at a time.

1. INTRODUCTION

From an ecological perspective, ants are the most ubiquitous and dominant of insects because of their sociality and cooperation (Wills & Landis, 2018; Borowiec et al., 2020). Roughly 14,000 ant species have been described and classified into 345 genera that represent 16 subfamilies (Bolton, 2022). The evolution of the Formicidae under the selection pressures exerted on each species is reflected in the diversity of foraging strategies. It is also common to observe changes in strategy within the same genus or even within the same species, reflecting the behavioral flexibility of ants (Passera & Aron, 2005).

The foraging strategies of ants are diverse, and can range from solitary to cooperative foraging in terms of the level of cooperation between workers during foraging and recruitment (Pol et al., 2011). Cooperative foraging strategies are all derived from a solitary foraging state, that is likely to have been similar to solitary foundress wasps and primitive Ponerinae, and have evolved independently several times within the Formicidae (Hölldobler & Wilson, 2009; Keller & Gordon, 2009; Plowes et al., 2013; Reeves & Moreau, 2019). The workers of solitary-foraging ants leave the nest, search for food and return, performing little or no nestmate recruitment (Plowes et al., 2013; Reeves & Moreau, 2019). In contrast, workers of cooperative forag-

ing species act as scouts that locate food items, then recruit other nestmates to help with food retrieval (Plowes et al., 2013; Lanan, 2014; Pol et al., 2015).

The ant species that eat the seeds of plants, collecting and storing them in underground chambers, are called granivorous or harvester ants (Taber, 1998). Although the latter term can refer to any ant species that harvest and consume seeds, it is most commonly applied to ants in the genera *Pogonomyrmex*, *Veromessor* and *Messor*. Genera of seed harvesting specialists include *Pogonomyrmex*, *Pheidole*, *Messor*, *Meranoplus*, and to a lesser extent *Aphaenogaster* and *Solenopsis* (Plowes et al., 2013). Harvester ants are one of the most intensively studied groups of ants. The majority of these studies focused on a small number of highly abundant harvester ant species, mainly *Pogonomyrmex* in the New World (Western United States, Central and South America), and *Messor* in the Old World (Mediterranean, Arabia and Africa) (Davidson, 1977b; Plowes et al., 2013).

Messor (subfamily Myrmicinae, tribe Pheidolini) is a genus with a moderate number of 126 described species (Plowes et al., 2013), including 23 in Morocco (Cagniant & Espadaler, 1997; Bolton, 2022). The genus is widely distributed across the Afrotropical, Oriental, Nearctic and Palearctic regions, with its highest diversity found in the latter (AntWeb, 2022), most commonly found in arid and

semi-arid areas, grasslands, and savannahs (Cagniant & Espadaler, 1997).

Foraging behavior has only been described for a few of the 104 Old World species of *Messor*. Ten species have been described as “group foragers”, as is the case with *M. barbarus*, which uses trunk trails, while the remaining species either use ephemeral foraging columns or are too poorly known to be classified. Three species are known to “forage individually”: *M. aciculatus*, *M. structor*, and *M. capitatus* (Plowes et al., 2013), although the latter, in some instances, adopt cooperative foraging (Arnan et al., 2010) with a trunk trails formation (Grasso et al., 1998). Trunk trails are long-lasting trails that persist for months or years, radiating outward from the nest in a dendritic pattern, and are typically cleared of debris or obstacles (Detrain et al., 2000; Lanan, 2014). At the end of the trail, the ants search individually. Foraging columns also radiate outward from the nest, but are shorter-lived than trunk trails, can lack cleared paths, and last just hours or days. The ants follow the foraging column to its end, thereafter fanning out and engaging in individual searching (Plowes et al., 2013; Lanan, 2014).

It has been demonstrated that the selection of seeds by ants is based on a number of factors, including seed size, seed distribution, and colony reserve levels (Reyes-López & Fernández-Haeger, 2002b; Azcarate et al., 2005). In their study on natural seeds, Detrain et al. (2000) found that the foraging efficiency of *M. barbarus* increased when colony activity was highest on trails heavily followed by the ants. In other words, on highly frequented trails of this species, seeds are brought to the nest in more significant numbers, more efficiently, and with a higher mean rate per worker. In the same study, they found that at short distances (close to the nest), the composition of ant retrievals tended to match local seed availability, suggesting an increase in selectivity by harvester ants with increasing distance between the food patch and the nest entrance. The same results were found for *M. arenarius* (Warburg, 2020; Segev et al., 2021), *M. semirufus*, and *M. ebeninus* (Segev et al., 2021). In short, these aspects encompass the attractiveness of seeds (in terms of the proportion of seeds collected by ants), the recruitment rate (the number of workers mobilized towards food sources), and the selection of food by ants (Reyes-López & Fernández-Haeger, 2001; Heredia & Detrain, 2005; Miller et al., 2020; Segev et al., 2021).

Central place systems are found for animals that feed their young, animals that store food, and social insects (Bernstein, 1975). The collective efforts of colony members determine the extent of colony-level foraging in social insects. It is consistent with Optimal Foraging Theory and Central Place theory that, in order to maximize foraging efficiency, they are able to allocate more foraging effort to relatively abundant food by recruiting more foragers, minimizing travel time during foraging trips and the energy expended in the process (Pyke et al., 1977; Reiss, 1987; Pyke & Starr, 2021). Moreover, at a specific distance from the central place (nest), Holder & Polis (1987) conducted optimal foraging experiments that demonstrated how de-

sert harvester ants, *Pogonomyrmex californicus*, maximize their net energy intake per unit time by preferentially harvesting more profitable food (= large and medium seeds); and as these seeds became less common, the relative abundance of less profitable (= small) seeds increased.

Experimental and theoretical studies have shown that group foragers find and exploit clumped and abundant resources more efficiently (Flanagan et al., 2012; Pol et al., 2015). On an hourly time scale, the intensity of foraging depends on the rate of food intake and on the activities of workers, such as patrollers, which are engaged in tasks other than foraging (Gordon, 1991).

We studied colonies from three sympatric species of *Messor*: *M. barbarus*, *M. maroccanus*, and *M. sanctus*. These three species are known to form long lines of individuals that follow trails leading to seed sources (Cerdan, 1989; Casellas et al., 2008; Hollis et al., 2015). They forage in large groups, moving along pheromone trails 10–15 m or more from the nest entrance (Cerdan, 1989; Hölldobler & Wilson, 1990; Hollis & Nowbahari, 2013). On a short-term scale, we hypothesized that seeds clumped in large piles can be collected more efficiently than scattered seeds by group-foraging ants of the Mediterranean harvester ants (*Messor*). In this context, we predicted that (1) the rate of food intake (foraging rate) will be higher on clumped seed patches than on scattered seeds. (2) Because of the link between the number of ants foraging and food supply (Gordon, 1991), we predicted, on a given seed source, that the foraging rate will develop according to the level of depletion of the source. (3) Considering that cooperative foraging strategies are more evolved than solitary foraging, we predicted that when seeds are distributed in multiple piles, ants will consume each pile before moving on to another.

2. MATERIAL AND METHODS

2.1 Study area

The studied colonies were located in a 200 m by 150 m plot (35°40.6285'N; 5°57.1409'W) in the grasslands of south-west of Tangier, North of Morocco (Fig. 1). The study was carried out during the period of July–August 2021.

We studied the morning foraging behavior of 15 colonies from three sympatric species of the genus *Messor*; five colonies each of *M. barbarus* (*barbarus* group), *M. maroccanus* (*aegyptiacus* group), and *M. sanctus* (*aegyptiacus* group). *M. barbarus* has a Western Mediterranean distribution, *M. maroccanus* is an Ibero-Moroccan endemic, and *M. sanctus* is characterized by a Mediterranean distribution (Borowiec, 2014; Guénard et al., 2017).

2.2 Field studies

In order to evaluate the efficiency of foraging behavior depending on resource distribution, we used a design similar to that of Davidson (1977b) and Flanagan et al. (2012). Additionally, when highly attractive artificial baits are used, Reyes-López & Fernández-Haeger (2001) found that *M. barbarus* seeks to minimize transport time to the nest by reducing the time invested in load selection. Considering the results of these studies, our experiment was designed to provide colonies with bait at short distances around the nest, thereby facilitating study of the short-term responses of the colonies to the variation in the availability and/or distribution of seeds. Thus, the formation of a direct foraging column between the bait and the entrance of the nest eliminates

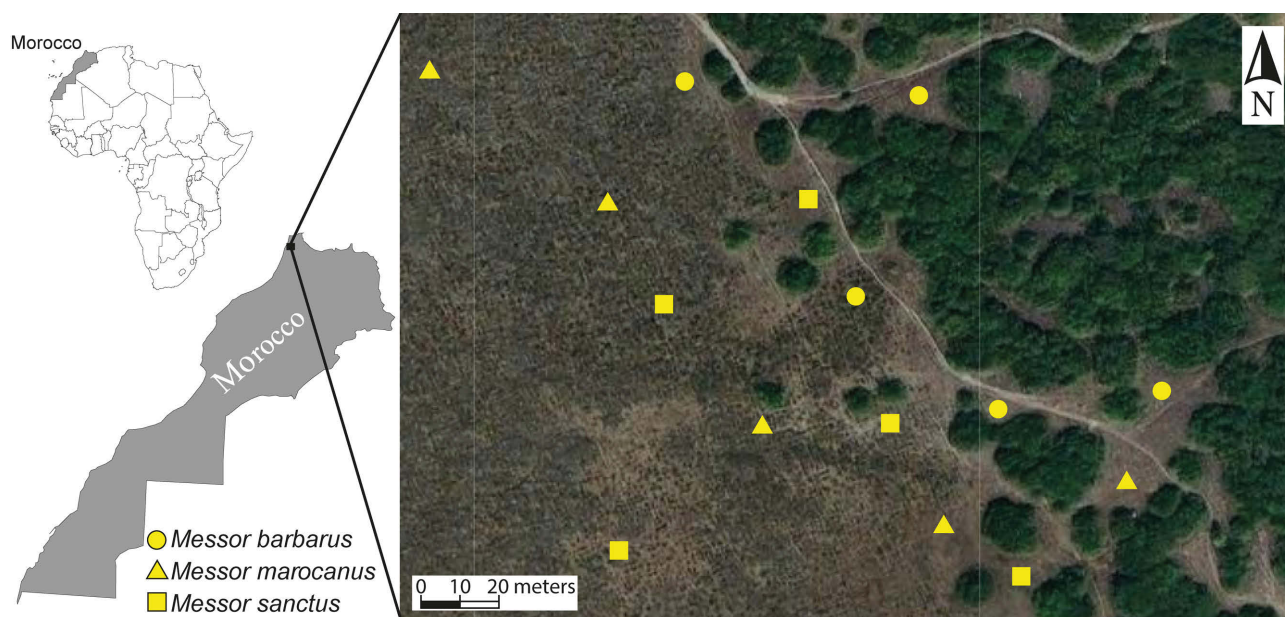


Fig. 1. Study area and location of the studied colonies.

the influence of seed-size selection and avoids any interference with the flow of ants on the trunk trail. Therefore, to prevent any influence of competition on our study, we conducted experiments within exclusion zones. These zones encompass the area surrounding a nest entrance from which all other colonies are entirely excluded, covering an area of radius between 20 and 150 cm for *M. barbarus* (Blanco-Moreno et al., 2014).

In prior research on *Messor* species, cafeteria experiments were conducted. These experiments involved placing seed baits at varying distances from the nest entrance, ranging from 30 cm for *M. bouvieri* (Retana et al., 1994) to 100 cm for *M. barbarus* (Reyes-López & Fernández-Haeger, 2002a). In our preliminary trials, we positioned seed baits at distances of 30 cm, 60 cm, 90 cm, and 120 cm from the nest entrance for each species, conducting three replicates for each species. However, for distances of 90 cm and 120 cm, over 50% of the baits remained undiscovered by the focal colony or were consumed by workers from other nests or species. Consequently, we selected a distance of 60 cm as the optimal placement for seed baits at the nest entrance. Using the same approach, seed baits ranged from 100 seeds for *M. bouvieri* (Retana et al., 1994) to 300 seeds for *M. arenarius*, *M. ebeninus* and *M. semirufus* (Segev et al., 2021). In our pilot trials, we placed baits composed of 300, 600 and 900 seeds (60 cm from the nest entrance) for each species, conducting three replicates. Notably, *M. sanctus* needed over 120 min (when the effect of temperature may not be perceptible on ant activity near the nests (Doblas-Miranda & Reyes-López, 2008)) to harvest baits comprising 600 and 900 seeds. Thus, we selected 300 as the optimal number of seeds per bait.

For each colony, we placed baits containing 300 barley (*Hordeum vulgare*) seeds, distributed in four ways: a single pile, two piles, three piles, or scattered. Piles and scattered seeds were placed 60 cm from the nest entrance (Fig. 2a,b,c), with the same density in each pile. To be able to assess the temporal variation in foraging rate of seeds collected from each of the piled distributions, the seeds were colored (food coloring) while conserving equal numbers of seeds per replicate: one pile of 300 red seeds, two piles of 150 red/green seeds, and three piles of 100 red/green/blue seeds.

We carried out a total of 60 replicates in a field experiment on five colonies from each of the three species (four distributions

for each colony: one, two, and three seed-pile baits in addition to scattered seeds). We never carried out more than one experiment per day on any single colony, and furthermore, experiments on the same colony were separated by at least four days to avoid the influences of seasonal endogenous factors related to the proximity to the production of alates (Díaz, 1992) or the loss of larger workers (Retana et al., 1994). We began observations each morning to coincide with the start of daily foraging activity at a soil temperature between 21 to 29°C to avoid its effect on ant activity (Gordon, 1983; Crist & MacMahon, 1991; Morehead & Feener Jr., 1998; Azcárate et al., 2007; Doblas-Miranda & Reyes-López, 2008; Baraibar et al., 2011; Flanagan et al., 2012; Solida et al., 2014).

The deposit of the bait was random except that it must not cross the trunk trails, and be in different positions for each replication in order to avoid for any memory effects (Letendre & Moses, 2013) and site fidelity (Fewell, 1990; Beverly et al., 2009). Patrolling workers move with frequent stops and direction changes, regularly inspecting encountered objects with their antennae, and are typically the first workers to leave the nest and search for food resources (Gordon, 1983). Experimental baits were placed after observing patrollers' activity near the nest entrance. An observer recorded the time each seed was brought into the nest with a timestamp using an Android application that was created for this study (allowing the observer to click on the button corresponding to the load transported by the ant and save the results at the end in .xlsx format), and which can be downloaded from supplementary data. We stopped observations either when a focal colony ceased foraging or when ants had collected all experimental baits, 60–120 min after the start of observations.

To evaluate the intensity of foraging once seeds have been discovered by the patrolling workers that are capable of recruitment, we calculated the foraging rate by dividing the total number of seeds retrieved by the number of minutes required to remove all seeds (Gordon, 1983). To account for variation in the number of foragers, we used a distribution of 300 scattered seeds as a bait control to normalize our observed foraging rates across experiments (Flanagan et al., 2012); see explanation in data analysis. The control bait was 60 cm away from the nest entrance (Fig. 2d).

To compare the seed intake from multiple sources of food at the same time for the three species, we placed an equal number

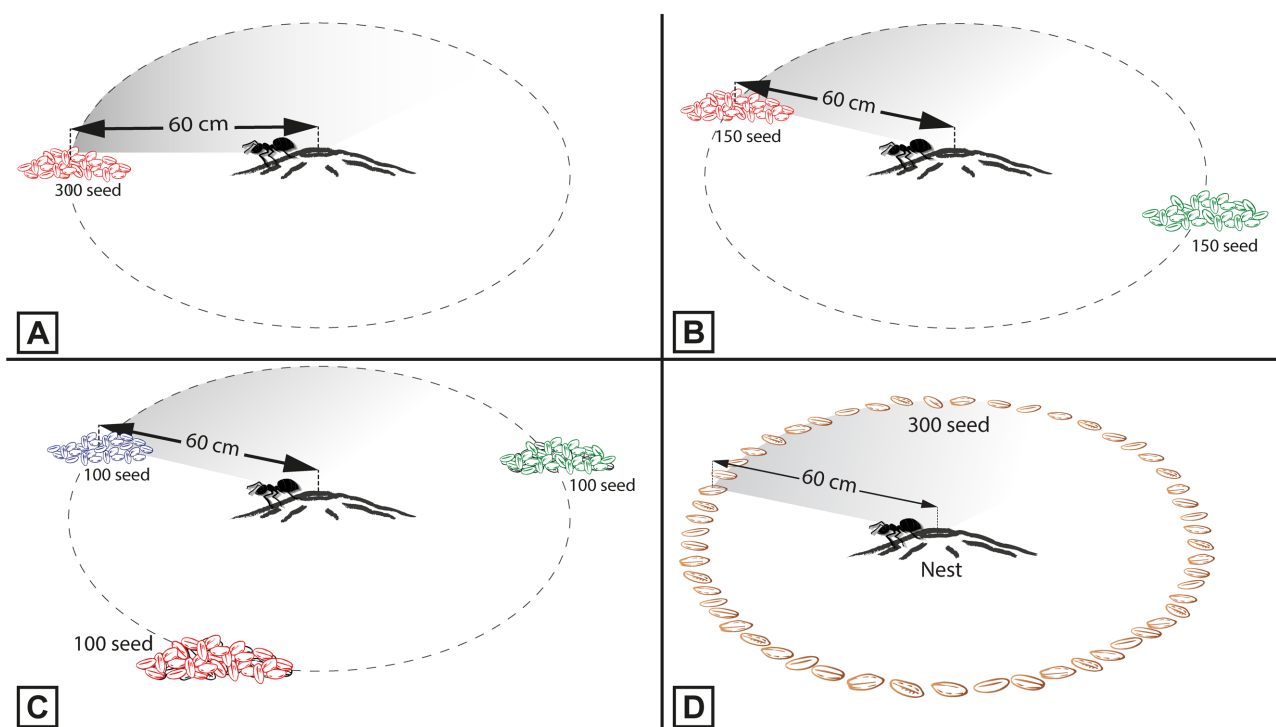


Fig. 2. Experimental design of four distributions of barley seeds (*Hordeum vulgare*) placed 60 cm from the nest entrance. (A) one pile of 300 red seeds, (B) two piles of 150 red/green seeds, (C) three piles of 100 red/green/blue seeds, and (D) 300 seeds scattered.

of seeds in piles of three colors. A test was conducted to verify if there was any inherent color-related bias impacting seed intake from the bait. To ensure equal opportunities for foragers to access different colors of seeds, 900 seeds were placed in a mix of three distinct colors – 300 red, 300 blue, and 300 green seeds. The color of each seed was noted after foragers had removed the first 300 seeds. This procedure was replicated nine times for each studied species.

Attractive seed baits may affect species and change their normal foraging activity (Davidson, 1977a). To test for these effects, we measured foraging rates for each species on unmanipulated naturally occurring seeds by recording the time required for the return of 300 laden foragers to the nest (unbaited) under the same conditions as for the baits.

2.4 Data analysis

To verify any potential biases in the results due to our experimental design, an independent-samples t-test was conducted to compare foraging rates on baited seeds against those observed on natural resources. Furthermore, a Kruskal-Wallis test was performed to assess the variability in seed intake from bait comprising seeds with different colors.

The foraging behavior of harvester ants can be divided into two largely distinct processes (Kunin, 1994). Accordingly, we divided the foraging time into two periods: the discovery time (the time taken for the first seed to be collected), and the seed collection period (the time between the collection of the first and the last seeds).

To compare seed collections from different pile sizes, we calculated the rate (Formula 1; FR = foraging rate) at which seeds are collected from each of the piled distributions (one pile of 300 seeds, two piles of 150 seeds, and three piles of 100 seeds).

$$(1) \text{ FR} = \frac{\text{Number of collected seeds}}{\text{Time (min)}}$$

The scattered bait seeds allowed us to calculate the normalized foraging rate: it describes the rate at which piled seeds are collected relative to scattered seeds within each experiment (Formula 2). The average distance between the seeds and nest, as well as the number of foragers active during experiments, were the same for random and piled seeds in each experiment (Flanagan et al., 2012). Regarding normalized foraging rates, the only parameter that changed was how clumped the distributions were. The scattered seeds served as a control for each experiment, allowing us to evaluate the effect of seed distribution on foraging rate for the three species (Flanagan et al., 2012). Therefore, these normalized foraging rates allowed us to avoid biased comparisons due to differences in the number of foragers from one colony to another and from one species to another.

$$(2) \text{ Normalized FR (piled seeds)} = \frac{\text{FR (piled seeds)}}{\text{FR (randomly scattered seeds)}}$$

A repeated measures design improved efficiency and allowed testing dependent \times independent variables (Guo et al., 2013). To establish whether seed distributions had an effect on discovery time, foraging rate, and normalized foraging rate for the three species, we conducted repeated measures ANOVA using SPSS Statistics 26.

To compare the temporal variation in foraging rate of the three species for one pile of 300 seeds, we calculated foraging rates and normalized foraging rates of 300 seeds divided into ten intervals (30 seeds per interval). Cumulative curves of seed collections are presented to compare the seed intake from three sources of food in the same time for the three species.

3. RESULTS

There was no significant difference in foraging rates on baited seeds (Mean = 10.75 seeds/min, SE = 1.01) versus natural seeds (Mean = 11.36 seeds/min, SE = 1.07) resources (t-test, $t(28) = 0.416, p = 0.681$). Therefore, our baits did

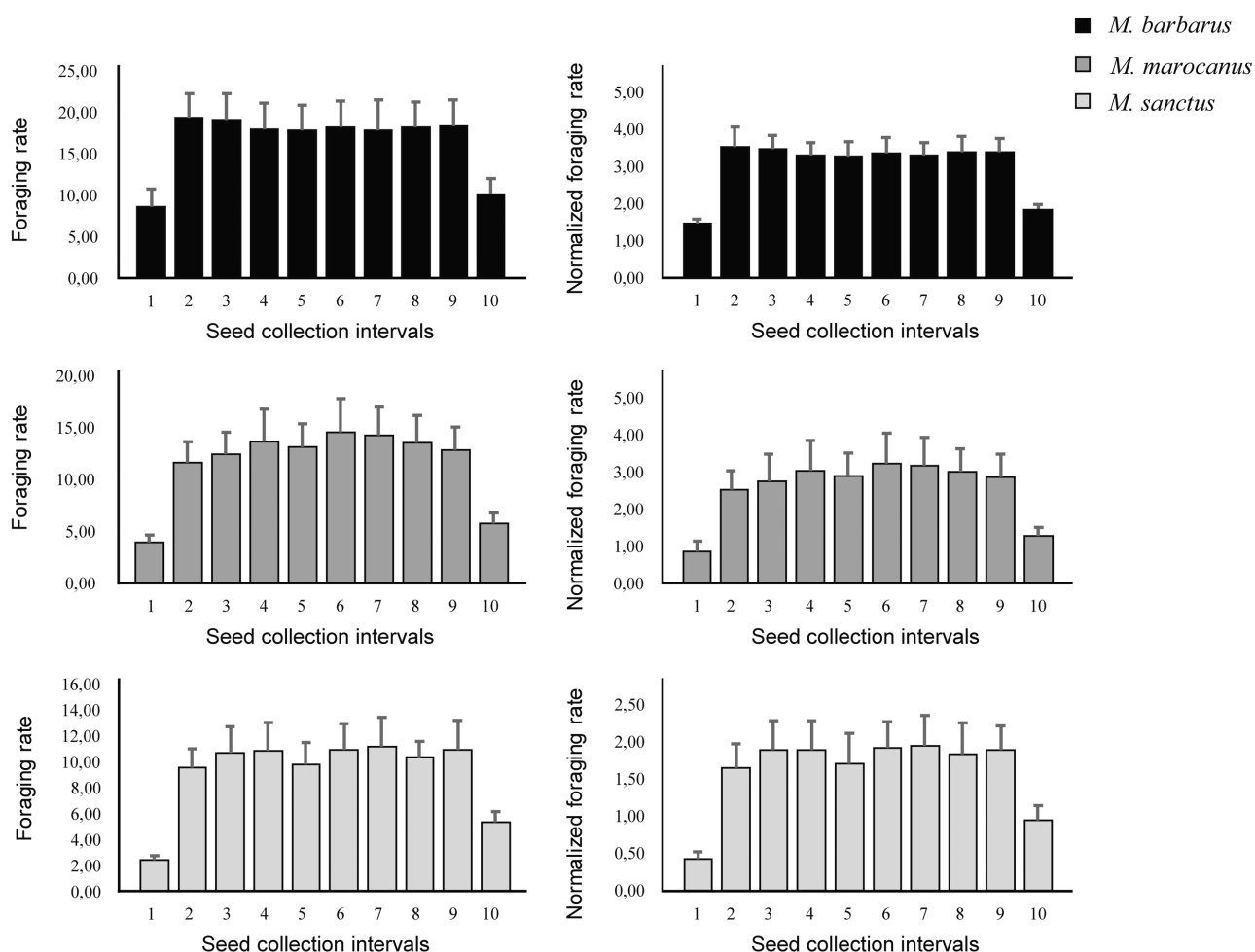


Fig. 3. Temporal variation in foraging rate (seeds/min) and normalized foraging rate for three species on a single pile of 300 seeds, divided across ten intervals of 30 seeds per interval.

not attract more foragers than the natural sources (Table 1). Furthermore, there was no color-related bias in the intake of seeds from baits with an equal number of mixed colored seeds (Kruskal-Wallis test, $H(2) = 0.401$; $p = 0.818$).

Among the three species, the foraging rate differed significantly (ANOVA $F(6,36) = 21.390$; $p < 0.001$). Foraging rates were highest in *M. barbarus*, intermediate in *M. maroccanus* and lowest for *M. sanctus*, and in each species, rates decreased as the seeds were more widely scattered in distribution (from seeds clumped in a single pile to those distributed in two or three piles). For all species, the foraging rate on scattered seeds was lower compared to rates on the bait distributions. The natural foraging rate showed

no significant differences (ANOVA $F(2,12) = 1.296$; $p = 0.309$) compared to the rate on the seeds clumped in one pile for all species (Table 1). Further, the normalized foraging rates of the three species differed significantly (ANOVA $F(4,24) = 3.840$; $p < 0.001$) in a similar pattern as for the respective foraging rates.

Within each seed distribution, discovery times were similar for all species (ANOVA $F(3,36) = 0.177$; $p = 0.859$), but were significantly different between distributions (ANOVA $F(6,36) = 15.013$; $p = 0.002$), with times becoming shorter when seeds were more scattered (Table 2).

Temporal variation in foraging rate and normalized foraging rate for each species and one pile of 300 seeds (Fig.

Table 1. Mean foraging rates (seeds/min) for natural seeds and baits (mean ± SE), number of experiments $n = 20$ for each species.

| Species | Baited seeds | | | Scattered seeds | Natural foraging |
|--------------------------|----------------|----------------|----------------|-----------------|------------------|
| | 1 Pile | 2 Piles | 3 Piles | | |
| Foraging rate | | | | | |
| <i>M. barbarus</i> | 15.319 ± 2.771 | 13.429 ± 1.386 | 11.309 ± 1.199 | 5.506 ± 1.023 | 16.189 ± 3.055 |
| <i>M. maroccanus</i> | 9.571 ± 1.497 | 8.231 ± 0.551 | 7.739 ± 0.428 | 4.665 ± 0.998 | 10.292 ± 1.517 |
| <i>M. sanctus</i> | 7.352 ± 0.964 | 6.607 ± 1.483 | 5.993 ± 0.651 | 5.862 ± 0.995 | 7.593 ± 0.514 |
| Normalized foraging rate | | | | | |
| <i>M. barbarus</i> | 2.790 ± 0.220 | 2.477 ± 0.291 | 2.082 ± 0.213 | – | – |
| <i>M. maroccanus</i> | 2.118 ± 0.503 | 1.820 ± 0.351 | 1.718 ± 0.367 | – | – |
| <i>M. sanctus</i> | 1.282 ± 0.265 | 1.156 ± 0.324 | 1.048 ± 0.222 | – | – |

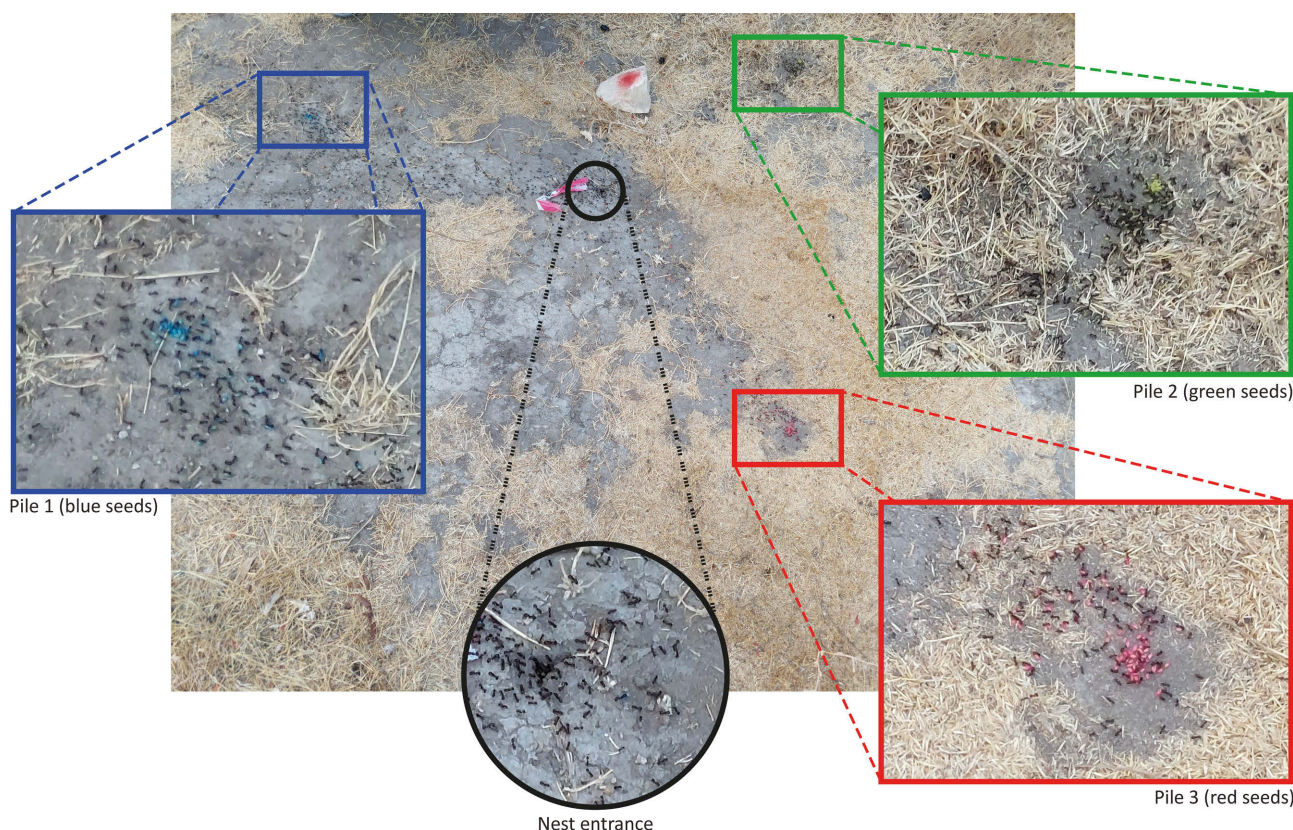


Fig. 4. *Messor maroccanus* retrieving seeds from three seed piles concurrently. Photo by A. El Boukhrissi.

3) was stable between seed nos 31–270. However, they were lower for the first and last 30 seeds.

Concerning the seed intake from multiple sources, *M. maroccanus* tended to retrieve seeds from several piles simultaneously (Fig. 4), while *M. barbarus* and *M. sanctus* retrieved seeds from the first pile before moving on to the second and then the third (Fig. 5).

4. DISCUSSION

The main study findings, for the three sympatric species of the genus *Messor* (*M. barbarus*, *M. maroccanus*, and *M. sanctus*) are that colonies forage more efficiently (higher foraging rates) on more clumped seeds. This suggests that foragers recruit more nestmates on clumped seeds, which increases foraging rates for these distributions. Also, normalized foraging rates were higher on more clumped seeds for all species, suggesting that the number of foragers in the observed colonies did not influence the foraging behavior of these colonies in response to seed distribution. For all three species, the discovery time to locate food sources

was similar, and the foraging rate was stable except for the beginning and the end of the formation of foraging columns. However, on multiples resources, *M. barbarus* and *M. sanctus* collected seeds from one resource at a time, whereas *M. maroccanus* could collect from several sources simultaneously.

For all studied species, the foraging rates were higher on more clumped seed distributions, confirming our first hypothesis. Andersen & Ashton, (1985) found that since the size of seed clumps influences removal rates in the short-term, these should reflect natural seed densities. Therefore, our result is in line with previous studies in which researchers found a positive relationship between foraging rates and both resource density and seed clumpiness (Davidson, 1977b; Taylor, 1977; Flanagan et al., 2012; Pol et al., 2015; Wenninger et al., 2016; García-Meza et al., 2021; Reyes-López & Fernández-Haeger, 2002a). This positive relationship can be explained by the increase in recruitment rate, which refers to the number of ants per unit of time that come to a food source to retrieve it after it has been discovered (Gordon, 1983). This recruitment behavior is particularly pronounced in the context of clumped seed patches, as evidenced by Cerdá et al. (2009) in their study of the gypsy ant, *Aphaenogaster senilis*. Their research demonstrated that group recruitment is employed to collect food that is not individually transportable, such as crickets and shrimps, as well as large seed piles, whereas small seed piles rarely elicited recruitment behaviors. On the contrary, more dispersed seeds offer fewer seeds per pile, and consequently they are completely consumed before reach-

Table 2. Mean discovery times in minutes for bait distributions of 1, 2 & 3 seed piles, and scattered seeds at 60 cm from the nest (mean ± SE), (number of experiments N = 20 for each species).

| Distribution of seeds | <i>M. barbarus</i> | <i>M. maroccanus</i> | <i>M. sanctus</i> |
|-----------------------|--------------------|----------------------|-------------------|
| 1 pile | 5.43±0.74 | 4.99±0.55 | 5.60±0.46 |
| 2 piles | 4.93±0.36 | 4.28±0.35 | 4.85±0.47 |
| 3 piles | 3.69±0.42 | 3.24±0.75 | 3.19±0.70 |
| Scattered | 3.52±1.85 | 3.06±1.51 | 3.14±1.86 |
| All treatments | 4.69±0.90 | 4.17±0.91 | 4.55±1.16 |

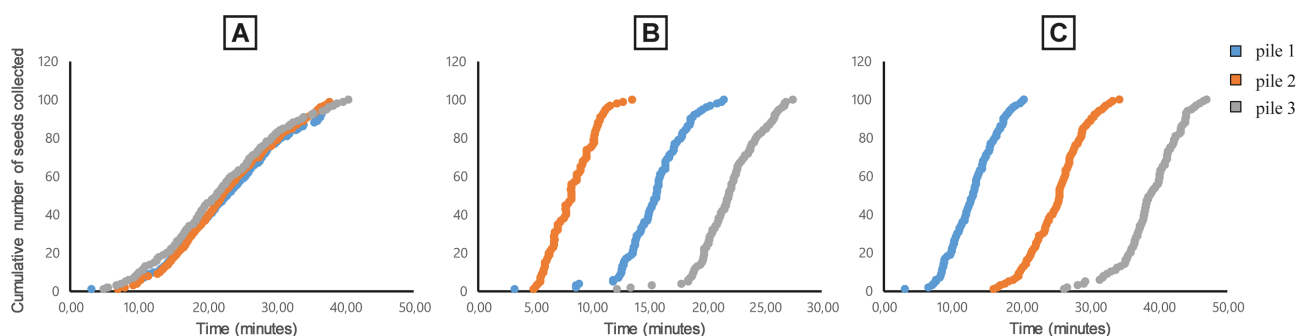


Fig. 5. Seed intake from one experiment (three piles of 100 seeds) for each species (A) *Messor maroccanus*, (B) *Messor barbarus*, (C) *Messor sanctus*.

ing the equivalent level of recruitment on distributions containing more seeds. This explanation is supported by studies of Wenninger et al. (2016) and García-Meza et al. (2021), who found that by conveying information between nestmates, colonies increased the number of active ants in patches with a greater density of resources. In addition, feedback on foraging activity dependent on food distribution and availability, carried out in the context of optimal foraging theory, allows the colony to regulate its foraging activity according to the current costs of desiccation in high temperature environments (Morehead & Feener Jr., 1998; Gordon et al., 2013).

Similarly, even with the normalizing of foraging rate (calculated relative to scattered seeds), we found that colonies of all species increased their foraging rate on more clumped seeds. It suggests that in our case, the difference in the number of foragers does not influence the foraging behavior of the colonies. This is in agreement with the results of Flanagan et al. (2012) on *Pogonomyrmex*, where large and small colonies allocate relatively similar proportions of foragers to large piles in order to harvest them faster. Moreover, Flanagan et al. (2011) found that the increase in foraging rate is indistinguishable across colonies ranging from 100 to 1000 foragers of *Pogonomyrmex*. However, these suggestions must be interpreted with caution because, in our study, the number of foragers was not measured, and so this factor could be neutralized if these species had similar numbers of foragers.

In our study, species identity did not influence discovery time, and the more the seeds were dispersed, the more time colonies needed to discover them. However, the foraging rates were lower for scattered seeds than for natural seeds or baits. This can be explained by considering that natural foraging is done on clumped seeds in foraging areas. Foraging trails end in areas showing higher densities of seeds (Detrain et al., 2000), and the same pattern is observed when seeds are clumped in baits. In both cases, once the source has been discovered, the seeds are collected without being affected by the discovery time. Reduced searching time may trigger the increase of foraging rates (Pol et al., 2015), whereas when foraging on scattered seeds, each seed must be discovered and collected independently, which decreases the foraging rate. In summary, discovery time acts on each seed when scattered, while it acts only on the first seeds collected from natural or bait clumps.

Our second hypothesis was partially verified because the foraging rate remained stable over the period of seed collection in all three species. However, there was an increase at the beginning and a decrease at the end of the formation of the foraging columns. These variations are explained by the action of recruitment mechanisms. At the colony level, from one hour to the next, colonies are able to respond quickly to an increase in food supply, by allocating more foragers from other task groups to retrieve the new food sources, and when food intake decreases, so does the number of foraging ants (Gordon, 1991). Thus, the recruitment of foragers is connected in a closed loop to the foraging activity outside the nest through feedback from the ants themselves (Pagliara et al., 2018). This suggests that after achieving a certain level of recruitment to a particular food source, the foraging activity remains consistent until the source is completely depleted.

Our third hypothesis was verified for *M. barbarus* and *M. sanctus*, but not for *M. maroccanus*. Recruitment for retrieving food may be more advantageous for ephemeral foods that can disappear or be taken by competitors (Lentendre & Moses, 2013). This result shows that these species have recourse to different strategies to make the most of the resources of the environment to outcompete others. In the first strategy, *M. barbarus* and *M. sanctus* exploit a resource before it is discovered by other competitors. In contrast, in the second strategy, *M. maroccanus* makes the most of all the resources available at the same time. In this way, the foraging behavior of *M. maroccanus* is positioned between that of the ancestral individual foragers (exploit multiple sources individually) and that of the more evolved group foragers (exploit single source cooperatively) (Hölldobler & Wilson, 2009; Plowes et al., 2013; Pol et al., 2015; Reeves & Moreau, 2019).

The way in which *M. maroccanus* exploits multiple seed piles could mean that their colonies have a higher proportion of scout ants that are constantly exploring the nest surroundings for new food sources, whereas in the case of *M. barbarus* and *M. sanctus*, the whole foraging force is concentrated on the first food source discovered. Consequently, it can be predicted that *M. maroccanus* is more opportunistic in its seed regime and has a broader diet niche than *M. barbarus* or *M. sanctus*. This difference in strategies, in response to the variation in distribution and abundance of resources, can be explained by the large ca-

capacity for behavioral flexibility shown by several *Messor* and *Pogonomyrmex* species (Cerde & Retana, 1994; Pol et al., 2015), which can shift between individual foraging and recruitment depending on the environmental conditions (Plowes et al., 2013).

In applying classic methodology, we have obtained highly interesting insights about the foraging behavior of three *Messor* species in response to variation in the distribution and abundance of their resources. Further development and application of such highly replicable and standardized methods should allow us to gain an even better understanding of the behavioral strategies of harvester ants.

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