



Influence of seed size and seed nature on recruitment in the polymorphic harvester ant *Messor barbarus*

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Abstract

In the polymorphic harvester ant *Messor barbarus*, the colony modulates response during foraging according to seed characteristics. The easiness of picking up small seeds (oat fragments or canaryseeds) shortens the time lapse between food discovery and the return of scouts to the nest, favouring the onset of recruitment and higher mobilisation rates than bigger seeds (whole oat). However, size is not the only criterion, as canaryseeds are preferred among small ones. A modulation of the trail laid by the first scouts also plays a role in the shaping of harvesting patterns and in the enhancement of recruitment towards small and/or preferred seed. This flexibility extends to the relative participation of the three worker sizes classes, which differs according to seed. *Media* are the most numerous at the foraging arena and largely responsible for trail-laying. *Minor* participate in seed harvesting and trail-laying, mostly when they can be efficient in carrying seeds, such as oat fragments. *Major* scarcely participate in harvesting and trail-laying, but are involved in the exploitation of bigger and/or preferred seed species. When faced with different seed species, *M. barbarus* seems thus to collectively adopt a “foraging time minimisation” rather than an “energetic gain per item harvested maximisation” strategy. Dynamics of foraging and division of labour between foragers of different sizes are related to both the workers’ ability to carry seed items, and the transfer of information to nestmates by trail-laying, all parameters that vary according to seed characteristics.

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1. Introduction

In harvester ants, foraging patterns depend both on characteristics of workers’ biology, such as foragers’

morphology and behaviour, and on those of resources available in the environment, notably seed species composition, size, abundance and spatiotemporal distribution (e.g. Mehlhop and Scott, 1983; Hobbs, 1985; Crist and MacMahon, 1992; Ferster and Traniello, 1995; Wilby and Shachak, 2000). It was also shown that competition can play, as well, an important role in the distribution of the foraging activity (e.g. Brown and Gordon, 2000).

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Several studies have investigated how harvester ants adjust their collective foraging responses to changes in seed availability. Concerning the spatial distribution of seeds, a more intense recruitment leads nestmates of *M. barbarus* (Detrain et al., 2000), *M. structor* (Hahn and Maschwitz, 1985), *M. pergandei* (Mehlhop and Scott, 1983) and *Pogonomyrmex* spp. (Bernstein, 1975; Hölldobler, 1976; Whitford, 1978; Crist and MacMahon, 1991a, 1992) to plants producing a large amount of seeds at a time or in concentrated patches. The recruitment intensity can also be adjusted according to the nest-source distance (Crist and MacMahon, 1991a, 1992; Díaz, 1992), and can result in higher numbers of foragers mobilised to nearer seed patches (Hölldobler, 1976; Taylor, 1977). Moreover, the spatial patterns of foraging trails can also be closely related to seed abundance. In *Pogonomyrmex* spp. (Rissing and Wheeler, 1976) and *M. pergandei* (Goss and Deneubourg, 1989), foraging trails change direction and length according to seed availability, and *M. barbarus* colonies form shorter but more ramified trails when seeds are locally abundant (López et al., 1993, 1994).

Furthermore, some studies have described diet selection at food sources according to the size/nature of naturally occurring seeds or seed baits (Crist and MacMahon, 1991a, 1992; Díaz, 1992; López et al., 1993; Taylor, 1977; Traniello and Beshers, 1991; Wilby and Shachak, 2000; Willott et al., 2000). In *Pogonomyrmex* spp. and *M. galla*, some seed species are preferred, and their selection is not solely related to their availability (Whitford, 1978; Gillon et al., 1984; Crist and MacMahon, 1991a, 1992), but probably also to their chemical properties, smell and/or caloric content (Nickle and Neal, 1972; Ferster and Traniello, 1995). Concerning seed size, foraging responses are very variable according to experimental conditions, ant species, and the range of seed sizes available. Notably, there is a morphological constraint on harvesting, since minimum and maximum limits of seed size exist, below and above which a forager cannot detect and/or carry the seed item. In *M. barbarus*, retrieval on natural foraging trails depends on seed weight, those of less than 0.4 mg being rarely chosen (Detrain and Pasteels, 2000). Furthermore, the intensity of recruitment can be related to seed weight, as shown in *M. capitatus* (Baroni-Urbani and Nielsen, 1990) and *P. occidentalis* (Taylor, 1977). Under controlled conditions, a more intense recruitment is reported towards smaller than bigger seeds

in *P. rugosus* (Hölldobler, 1976), while colonies of *Pogonomyrmex* spp. recruit more nestmates to baits of medium-sized seeds among those offered (Davidson, 1978).

Species with a polymorphic worker caste show an additional degree of flexibility and variability in their foraging strategies. Actually, in these species, the characteristics of food sources cannot only influence the recruitment's intensity, but also the relative participation of castes in this process (Itzkowitz and Haley, 1983). In harvester species showing a continuous polymorphism, like *M. barbarus*, considerable effort has been devoted to the study of foraging strategies in natural or semi-natural conditions (e.g. Baroni-Urbani and Nielsen, 1990; Traniello and Beshers, 1991; Retana and Cerdá, 1994; Ferster and Traniello, 1995; Reyes-López and Fernández-Haeger, 2001). However, relatively little attention was given to the behavioural mechanisms that tune their foraging dynamics according to the characteristics of seed baits, such as the modulation of trail-laying intensity. In this respect, our knowledge of the recruitment system in *Messor* species is still rather fragmented and has been essentially devoted to the identification of glandular sources of pheromones (Hahn and Maschwitz, 1985; Grasso et al., 1998, 1999; Heredia and Detrain, 2000).

The present paper follows an intensive approach that deepens in the knowledge of social mechanisms of seed harvesting: the trail recruitment. The novelty of this study is to analyze the influence of seed size and seed nature on information transfer and cooperation during resource exploitation, taking into account the different morphological worker castes. To do this, we first study, in the harvester ant *M. barbarus*, the dynamics of food recruitment towards baits of seeds differing in size and/or nature. Secondly, we investigate how differences in the laying of chemical trail and in the retrieval of seeds at the individual level can be related to collective foraging responses. Finally, we highlight the relative participation of *minor*, *media* and *major* workers in recruitment dynamics and trail-laying behaviour, according to seed size and seed nature.

2. Materials and methods

M. barbarus is a common seed predator of the grasslands of the Mediterranean basin. Their nests can be

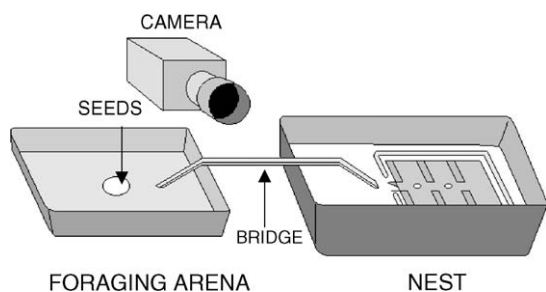


Fig. 1. Experimental set-up.

easily located in the field by the clearly defined network of foraging trails. *M. barbarus* workers present a continuous polymorphism, and three size classes can be recognised according to body length: *minor* (<5 mm); *media* (5 < *x* < 10 mm); *major* (>10 mm) (Chrétien, 1996; Heredia and Detrain, 2000).

Colonies were from Vidauban (South-eastern France) and reared in plaster nests in the laboratory. Nests (20 cm × 30 cm × 0.3 cm) were divided in three interconnected chambers (16 cm × 8 cm × 0.3 cm) covered by a red glass plate. They were reared under 22 ± 3°C, a relative humidity of 60%, and a photoperiod of 12 h-light per day. The experimental colonies were composed of about 1650 workers, with 38% of *minor*, 55% of *media* and 8% of *major*. These colonies comprised the workers found both along foraging trails, and in excavated nest chambers, confidently reflecting the natural caste distribution in the field. The caste-ratio was stable between tested colonies (Kruskal–Wallis test; *p* > 0.05, *n* = 9). Colonies were regularly fed a brown sugar solution (1 M) and a mix of seeds (canaryseed 36%, oat 33%, rapeseed 18%, millet 6%, hempseed 5%, linseed 3%), which were supplemented twice a week with cockroaches (*Periplaneta americana*).

The experimental set-up consisted in a foraging arena (37 cm × 22 cm) connected to the nest by a cardboard bridge (30 cm × 1 cm). A camera was placed perpendicularly to the middle of the bridge, focusing on 4 cm of it (magnification of 5×), and recording for 90 min (Fig. 1).

Six days before each experiment, colonies were deprived of sugar solution, cockroaches and seeds. This starvation procedure allowed us to work under controlled conditions, by preventing foragers to access not

only what constitutes their regular diet (i.e. seeds), but also nutrients that they occasionally exploit in the field (i.e. dead insects or nectar). Two days before testing, nests were connected to the arena, allowing foragers to explore it. After this starvation period, a recruitment was launched to a seed source. The choice of tested seed species was primarily guided by the need to compare food items of controlled size and similar shape, of which the weight stands within the range of seeds actually retrieved by *Messor* in the field (Detrain and Pasteels, 2000).

In the first set of experiments, oat (*Avena sativa*) seeds were offered. Seeds weigh 30.3 ± 6 mg, and measure 7.1 ± 0.6 mm length and 2.7 ± 0.4 mm width, on average (*n* = 30). In order to understand the influence of seed size on the recruitment dynamics of *M. barbarus*, comparative experiments were carried out with whole or with fragments of oat seeds. For that, seeds were crushed with a coffee mill and sifted with a metallic ASTM sieve with a 1.4 mm² mesh, resulting in oat fragments of 5 ± 1.2 mg (*n* = 30).

In the second set of experiments, we investigated how, besides size, the species and quality of seeds can alter the global foraging dynamics of *M. barbarus*. Therefore, a mix of canaryseeds (*Phalaris canariensis*) and whole oat seeds was offered in the same bait. Canaryseeds have approximately the same weight (6.5 ± 1.4 mg, on average, *n* = 30) and the same size (5 ± 0.3 mm length, 2.1 ± 0.2 mm width, on average, *n* = 30) as the oat fragments described above. Moreover, both seeds species have about the same composition: 20% of proteins, 65% of carbohydrates and 10% of lipids (Matz, 1991; Abdel-Aal et al., 1997).

Each experiment started with the introduction of a Petri dish (Ø 5 cm) in the foraging arena, presenting either: (1) a monospecific source containing 5 g of whole oat seeds; (2) a monospecific source containing 5 g of oat fragments; (3) a monospecific source containing a mix of 2.5 g of whole oat seeds and 2.5 g of oat fragments; or (4) a bispecific source containing a mix of 2.5 g of whole oat seeds and 2.5 g of canaryseeds. In mixed baits, items were concentrated and touching each other, so that foragers had the same probability of contacting both seed types at the source.

For each type of source, different groups of three different colonies were tested twice (*n* = 6 replicates). The two tests with the same colony were separated by at least 7 days.

The trail-laying behaviour of foragers was observed as they walked over the bridge to the nest. A contact between the tip of the worker's abdomen and the bridge was considered as a trail-laying behaviour. For each forager observed, the individual intensity of trail-laying was expressed by the percentage of images in which an abdomen-bridge contact was observed. Workers' mobilisation indexes were calculated as follows: for one caste, the number of workers at the arena (number of workers going to the arena minus number of workers going to the nest) was noted every 5 min and summed to the previous value. The cumulative final value, obtained after 90 min of observation, was then divided by the number of workers of this caste in the colony before the experience. Finally, these values were averaged over the six replicates. The presence rate of each caste was assessed by measuring the number of workers at the foraging arena every 5 min over 90 min. For each experimental condition, every 5 min' measure was averaged over the six replicates. The cumulative biomass of fragments and whole oat seeds was calculated as follows: for one seed size, the biomass harvested was noted every 15 min and summed to the previous value. The cumulative final value, obtained after 90 min of observation, was the average over the six replicates.

2.1. Data analysis

The number of samples being small, non-parametric statistical tests were used. The Kruskal–Wallis test was used to compare several groups of data, and was followed, when a significant difference was found, by the Dunn's post-hoc multiple comparisons test. The Mann–Whitney test was used to compare two groups of data. All p -values above 0.05 were considered not to be statistically significant.

3. Results

3.1. Recruitment dynamics and the role of trail-laying by scouts

Before the introduction of seeds, the presence rate of workers at foraging arenas is equivalent between the four sources (Kruskal–Wallis test, $p = 0.56$). However, as soon as seeds are presented, foraging responses vary according to sources (Fig. 2). The mobilisation

index towards whole oat seeds is weak but tends to increase in the presence of oat fragments, presented alone or in a mix (Table 1, column 1). Moreover, the higher mobilisation is favoured by a shorter time spent by foragers at the arena when oat fragments are proposed (287.2 ± 282.5 s, $n = 83$ for oat fragments, and 402.1 ± 339.8 s, $n = 60$ for whole oat, Mann–Whitney test, $p = 0.02$). Smaller seed items seem thus to enhance the harvesting response of *M. barbarus*. As a result, despite their low weight per item, compared to whole seeds (oat fragments, 5 mg; whole oat, 30 mg), the total biomass of oat fragments harvested was similar to that observed for whole items, at the beginning of the foraging recruitment (Fig. 3).

The highest recruitment response is elicited by the bispecific mix of whole oat and canaryseeds, since this mobilisation index is more than four times higher than that observed for whole oat seeds alone (Dunn's test, $p < 0.05$). The mobilisation index towards the bispecific mix tends also to be higher than that observed for the monospecific one containing oat fragments (Dunn's test, NS). Thus, there is an enhanced interest of *M. barbarus*' colonies for canaryseeds, which is due less to their small size than to their nature.

When considering the entire observation period, the percentages of trail-laying workers are equivalent between seed sources, and range from 37 to 50% of all workers going to the nest (Kruskal–Wallis test, $p = 0.32$). However, when considering only the first workers returning to the nest after having discovered the source, the workers' probability of laying a trail tends to vary according to seeds' size and nature. Actually, in the presence of oat fragments or the bispecific mix, the percentages of trail-layers among the 5 first returning workers are up to three times higher than those observed for the whole oat source or the monospecific mix (Kruskal–Wallis test, $p = 0.05$) (Table 2). The individual marking intensities of the 5 first trail-layers tend, as well, to be stronger than those observed for the other seed sources (Kruskal–Wallis test, $p = 0.61$). Moreover, these two sources tend to elicit up to five times faster returns of the first scout to the nest (Kruskal–Wallis test, $p = 0.46$). In the case of oat fragments, this first scout elicit 2.3–4.5 times higher numbers of nest exits in the 5 min following her arrival in the nest (Kruskal–Wallis, $p = 0.1$), resulting in a particularly fast mobilisation of nestmates towards the arena. This high trail-laying intensity, associated

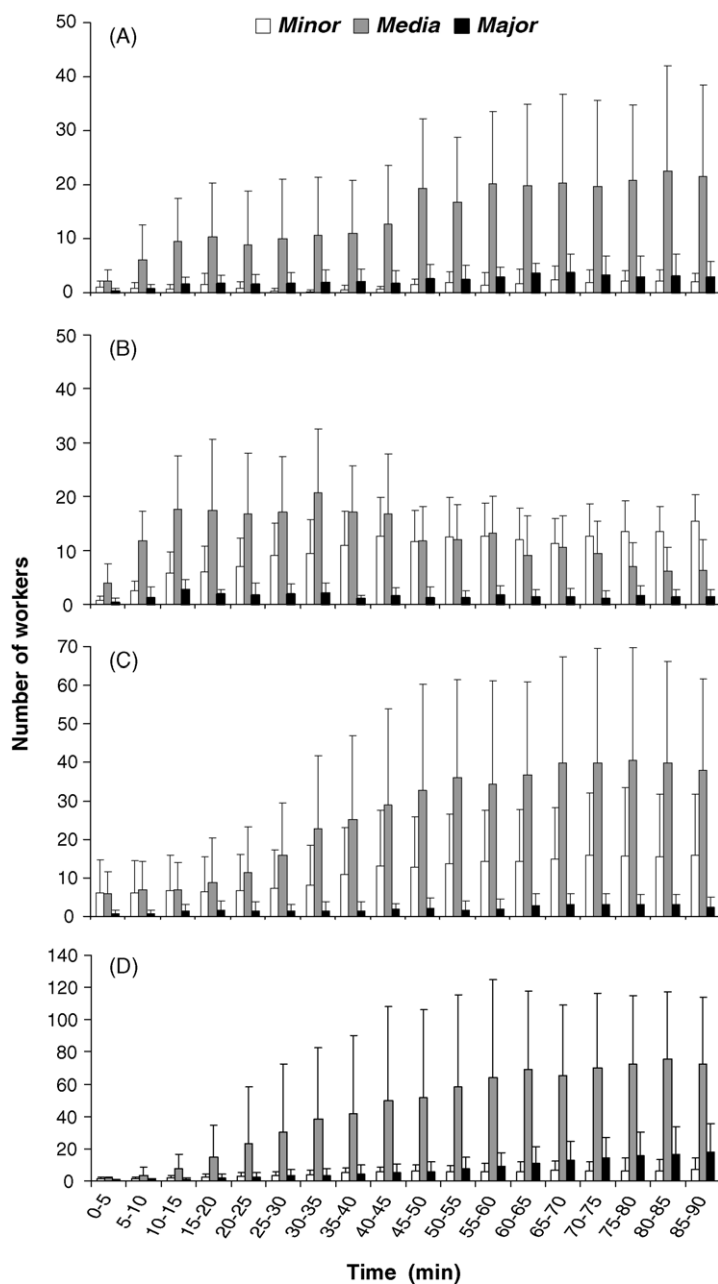


Fig. 2. Temporal evolution of the number of workers of each caste at the foraging arena according to seed sources: (A) whole oat; (B) oat fragment; (C) monospecific mix; (D) bispecific mix. Means (\pm S.D.), $n=6$.

with fast returns of the first scout to the nest explains the quickness and/or the high indexes of workers mobilised towards sources of oat fragments or to the bispecific mix (Fig. 2 and Table 1). Hence, the first scouts play

an important role in the global dynamics of recruitment: their trail-laying intensity varies with the size and nature of discovered seeds, these differences being attenuated in the course of recruitment.

Table 1
Mobilisation indexes of workers towards the foraging arena

Seed source	All castes together	Minor	Media	Major
Whole oat	12.1 (\pm 5.8) a	2.5 (\pm 1.4) a	18.2 (\pm 9.4) a	12.1 (\pm 5.1)
Oat fragment	31.8 (\pm 29.4) ab	12.6 (\pm 7.8) b	45.5 (\pm 45.1) ab	19.9 (\pm 18)
Monospecific mix	20.2 (\pm 12.8) ab	7.1 (\pm 5.7) ab	30.8 (\pm 19.7) ab	8.4 (\pm 4.3)
Bispecific mix	53.4 (\pm 33.1) b	5.9 (\pm 4.7) ab	86.7 (\pm 45.6) b	45.9 (\pm 50.6)
Kruskal–Wallis tests	$p=0.02$	$p=0.03$	$p=0.01$	$p=0.26$

For details about the calculation of these indexes see Section 2. Mean percentages (\pm S.D.), $n=6$. Within a column, means sharing the same letter are not significantly different (Dunn's tests, $\alpha=0.05$).

Table 2

Percentages of trail-layers among the five first workers returning to the nest after having contacted each seed source; moment of return to the nest of the first trail-layer (time between the contact with seeds and the arrival at the nest entrance) and number of exits from the nest she elicited within 5 min; intensities of individual trail-laying of the first 5 trail-layers returning to the nest

Seed source	% of trail-layers	Return to the nest (min)	Number of exits	Trail-laying intensity (%)
Whole oat	33.3 \pm 24.2	13.3 \pm 17.3	11 \pm 7.9	16.7 \pm 15
Oat fragment	63.3 \pm 29.4	3 \pm 2.6	24.8 \pm 15	26.3 \pm 26.9
Monospecific mix	20 \pm 12.7	15.2 \pm 16.4	9.3 \pm 8.3	16.4 \pm 11
Bispecific mix	53.3 \pm 35	9.3 \pm 9.2	5.5 \pm 2.7	20.6 \pm 17.4
Kruskal–Wallis tests	$p=0.05$	$p=0.46$	$p=0.1$	$p=0.61$

Means (\pm S.D.), $n=6$.

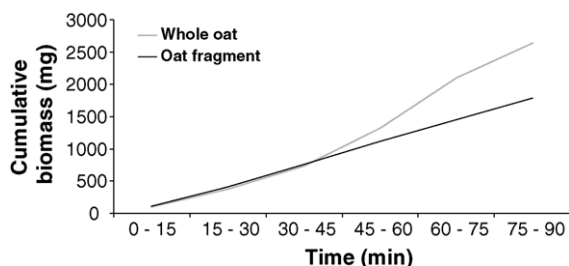


Fig. 3. Temporal evolution of the mean total biomass retrieved by workers from a source containing either whole oat seeds or oat fragments, $n=6$.

We also studied whether the fact of carrying a seed could influence a worker's probability to lay a trail. Thus, we counted the number of trail-layers among the first 10 seed-carriers and the first 10 non-carriers,

in the flow of workers returning to the nest. Our results show that, whichever the seed source, the number of trail-layers among seed-carriers is equivalent to that among non-carriers (Mann–Whitney tests, NS), which means that seed carrying does not influence the trail-laying behaviour of the first workers returning to the nest (Table 3). From then on, the mere retrieval of seeds cannot explain the higher trail-laying of scouts observed towards baits containing oat fragments or canaryseeds.

3.2. Mobilisation of castes and relative participation in trail-laying

Media are always among the first mobilised workers and form the majority of the population at the foraging arena (Fig. 2A–D). Their mobilisation indexes are

Table 3

Percentages of trail-layers among the 10 first workers carrying and not carrying a seed back to the nest

Seed source	Carriers ($n=10$)	Non-carriers ($n=10$)	Mann–Whitney tests
Whole oat	46.7 (\pm 25.8)	41.7 (\pm 18.3)	$p=0.75$
Oat fragment	53.3 (\pm 25)	50 (\pm 21)	$p=0.94$
Monospecific mix	40 (\pm 21)	38.3 (\pm 11.7)	$p=0.75$
Bispecific mix	50 (\pm 27.6)	55 (\pm 32.1)	$p=0.75$

Means (\pm S.D.), $n=6$.

always higher than those observed for *minor* or *major*, whichever the seed source offered (Table 1).

When whole oat seeds are presented, *media* are mobilised within the first 5 min, already forming the majority of the foraging arena population (Fig. 2A). *Major* appear later, and their number increases slightly over time. Even if their mobilisation index is close to that of *media* (Table 1) (Dunn's tests: *minor* vs. *media*, $p < 0.01$; *minor* versus *major*, NS; *media* versus *major*, NS), this caste is less present in it, because of their small number in the colony (see Section 2). Even representing 1/3 of the colony population, the number of *minor* at the arena remains low all over the recruitment process, when big oat seeds are proposed.

When fragments of oat seeds are offered, both *media* and *minor* are quickly mobilised (Fig. 2B). During recruitment, however, *minor* become more numerous than *media* at the arena. Their increase at the arena, despite the fact that the mobilisation index of *minor* tends to remain lower than that of *media*'s (Table 1) (Kruskal–Wallis test between the three castes, $p = 0.23$), can be explained by the 1.6 times longer time spent by *minor* at the arena, compared to *media* (360.3 ± 396.1 and 229.5 ± 208.4 s, respectively; Kruskal–Wallis test between the three castes, $p = 0.13$). Few *major* are present at the foraging arena during recruitment.

The monospecific mix of whole and fragmented oat seeds mobilises a similar number of *minor* and *media* at the beginning of the observation period (Fig. 2C). During the recruitment process, however, *media* become more numerous than *minor* at the arena and show a higher mobilisation index (Table 1) (Dunn's tests: *minor* versus *media*, $p < 0.05$; *minor* versus *major*, NS; *media* versus *major*, NS). *Major* are rare at the foraging arena, their mobilisation index being very low.

In the presence of the bispecific mix containing whole oat and canaryseeds, *media* are numerically dominant at the foraging arena (Fig. 2D). The dominance of *media* at the arena is related to a very high mobilisation index (Table 1) (Dunn's tests: *minor* versus *media*, $p < 0.01$; *minor* versus *major*, NS; *media* versus *major*, NS). *Major* also show a high mobilisation index towards the arena, this caste probably being drawn out of the nest in the high flow of exiting workers. Concerning seed retrieval, we evidence a size-matching phenomenon among *M. barbarus*' workers. Indeed, while whole seeds account for only 33% of the items retrieved by *media*, they represent up to 73% of the items harvested by *major* (Heredia and Detrain in prep.). Concerning *minor*, their mobilisation index is particularly low towards this bispecific mix, from which they harvest exclusively oat fragments.

For the same seed source, the percentages of trail-laying workers within *minor* and *media* are equivalent, while *major* are globally less involved in this task (Table 4).

Media are, in all cases, responsible for the majority of the trail-laying (Table 5), for this caste is numerically dominant in recruitment flows. It is noteworthy that the probability for *media* to lay a trail does not change with seed sources (Kruskal–Wallis test, $p = 0.33$) (Table 4). When oat fragments, alone or mixed, are proposed, *minor* actively participate in trail-laying (Table 5), and their probabilities of performing this behaviour are then high, in particular compared to *major*'s (Table 4). Because of their small number in recruitment flows, *major* weakly contribute in trail reinforcement (Table 5), their probability of performing this task being moreover not influenced by seed source (Table 4).

Table 4
Percentages of trail-layers within each caste

Seed source	<i>Minor</i>	<i>Media</i>	<i>Major</i>	Kruskal–Wallis tests
Whole oat	55.2 (± 26.8) ab	49.9 (± 16.5)	45.7 (± 29.8)	$p = 0.95$
Oat fragment	60.4 (± 20.6) a‡	42.9 (± 8.1) †*	10.7 (± 13) *	$p = 0.004$
Monospecific mix	52.3 (± 14.5) ab	35.7 (± 11.5)	28.4 (± 37.2)	$p = 0.05$
Bispecific mix	27.2 (± 16.4) b	43.4 (± 15.5)	15 (± 23.5)	$p = 0.13$
Kruskal–Wallis tests	$p = 0.04$	$p = 0.33$	$p = 0.18$	

Means (\pm S.D.), $n = 6$. Within a column or range, means sharing the same letter or symbol (respectively) are not significantly different (Dunn's tests, $\alpha = 0.05$).

Table 5
Relative contribution of each caste in the laying of a recruitment trail

Seed source	Minor	Media	Major	Kruskal–Wallis tests
Whole oat	7.9 (\pm 3.1) a	85 (\pm 8.7) b	7.1 (\pm 7.2) a	$p = 0.0028$
Oat fragment	19.9 (\pm 7.5) ab	78.9 (\pm 7.1) a	1.2 (\pm 1.2) b	$p = 0.0005$
Monospecific mix	13.3 (\pm 1.7) ab	82.4 (\pm 5.9) a	4.3 (\pm 6.9) b	$p = 0.0015$
Bispecific mix	3.6 (\pm 3.2) a	95.9 (\pm 2.6) b	0.6 (\pm 1.2) a	$p = 0.0014$

Mean percentages (\pm S.D.), $n = 6$. Within a range, means sharing the same letter are not significantly different (Dunn's tests, $\alpha = 0.05$).

4. Discussion

4.1. Chemical trail and recruitment dynamics

Several studies have pointed out differences, within the harvester ant genera *Messor* and *Pogonomyrmex*, in foraging responses according to resources, as well as preferences for certain seed species. Colonies choices have been related to the local seed availability or the fill state of granaries in the nest (Whitford, 1978; Mehlhop and Scott, 1983; Gillon et al., 1984; Hobbs, 1985; Crist and MacMahon, 1991a, 1992; Reyes-López and Fernández-Haeger, 2002). Measures like number of workers at sources or on trails were often carried out in the frame of the optimal foraging theory and associated with parameters of seed sources (Baroni-Urbani and Nielsen, 1990; Bernstein, 1975; Crist and MacMahon, 1991a,b, 1992; Davidson, 1978; Detrain et al., 2000; Díaz, 1992; Taylor, 1977; Traniello and Beshers, 1991; Whitford, 1978).

When studying ants' foraging strategies, it can be useful to also focus attention on communication and recruitment processes that shape the colony choice of a seed patch, as well as seed-harvesting dynamics. In social insects, like ants, a key element of recruitment takes the form of a positive feedback that is the active transmission of information brought back to the nest and shared with nestmates. In harvester ants, such information transfer can be implemented through the use of a recruitment trail (Heredia and Detrain, 2000), the perception of retrieved seeds by workers inside the nest (pers. obs.), as well as stridulation [as observed in many *Messor* species (Hahn and Maschwitz, 1985; Baroni-Urbani et al., 1988; Grasso et al., 1999), including *M. barbarus* (Cerdan, 1989; Hernández et al., 2002)]. The prevailing role of the recruitment trail on the emergence of colony foraging patterns and its modulation according to available resources is well known in many

ant species (reviews in Hölldobler and Wilson, 1990; Detrain et al., 1999). Hence, how the proportion of trail-layers among scouts, their individual laying intensity, as well as the number of exits elicited by them vary according to the characteristics of discovered seeds, is of the utmost importance to understand *M. barbarus*' collective resource exploitation. Our results on *M. barbarus* strongly suggest that the first scouts returning to the nest actually tune their trail-laying behaviour and differ in their time of return to the nest, according to seed size or nature. The resulting onset and growth of recruitment dynamics unexpectedly evidence that resource exploitation was not readily concentrated on seed sources of higher energetic yield per item. Besides, it highlights the need to consider the time scale of observations, as well as time constraints on seed retrieval, before giving functional interpretations to seed harvesting strategies. This is further detailed in the next two sections.

4.1.1. Influence of seed size

Some studies have brought to the fore the importance of weight/size of available seeds on the number of workers mobilised towards foraging arenas, as well as on the choice of source by colonies of harvester ants, like *Pogonomyrmex* spp. or *Messor* spp. (Hölldobler, 1976; Taylor, 1977; Davidson, 1978; Baroni-Urbani and Nielsen, 1990). As most studies on *Messor* species were carried out under natural conditions, harvested seeds of different sizes belonged to different species, which prevented the identification of the respective impact of seed size and seed nature on the foraging behaviour of ants (Detrain and Pasteels, 2000; Willott et al., 2000; Reyes-López and Fernández-Haeger, 2002). Our results show that, in *M. barbarus*, recruitments' dynamics actually vary according to the size of available seeds. Although whole oat belongs to the weight range of seeds that can be foraged by *M. barbarus*

(Detrain and Pasteels, 2000), the mobilisation index towards this seed is unexpectedly low and tend to be inferior to that observed for oat fragments. Similar results were obtained in *P. rugosus*, whose workers are less mobilised towards big seeds than to small ones (Hölldobler, 1976). In *M. barbarus*, the trail leading to oat fragments mobilises three times more workers than that leading to whole seeds. Three concurrent effects are at work: first, the exploitation of a seed patch rely on amplification processes, such as recruitment trail, in which the latency times of workers coming back from the foraging arena seems to be function of seed size. In this respect, the easiness of picking up oat fragments, due to their small size shortens the time lapse between food discovery and the return of the scout to the nest, and hence favours the onset of recruitment; second, the quick mobilisation of workers is favoured by the fact that foragers tend to spend a shorter time at the arena when oat fragments are proposed; finally, the tendency to higher and quicker trail-laying behaviour observed in the first workers returning to the nest elicits a more intense recruitment to small seed fragments compared to whole ones. However, it is noteworthy that the probability, for a worker, to lay a trail is not influenced by its ability to carry a seed, neither at the beginning nor throughout the recruitment process. As in many species of the *Pogonomyrmex* genus (Hölldobler, 1976), workers of *M. barbarus* can carry a seed and lay a trail at the same time. The proportion of workers laying a trail is therefore independent of the easiness of picking up small seeds.

One may question the adaptive value of such stronger and quicker recruitment to small-sized seeds compared to larger ones, which, associated with shorter transport times to the nest, would lead, in the case of competition between sources, to the selection of small items patches. At first sight, this result may seem counterintuitive since, at the individual level, one oat fragment is always less energetically valuable than one whole seed. However, when considering the colony level, a patch consisting of several small items that are easily and quickly harvested can yield a benefit per time unit similar to that of a patch of larger items, hard to carry. Actually, we show that, in terms of biomass, the exploitation of an oat fragment patch is as profitable to the colony as a whole oat seed source, at least over short timescale. This confirms that one major criterion in seed selection appears to be the time spent in

its harvesting, workers aiming at optimising the energetic flow gathered per time unit. Since for harvester ants the energetic gain provided by a seed, whichever its size and/or energetic content, is always higher than the cost of its harvesting, the time minimisation in seed harvesting is of the utmost importance in *M. barbarus*, like in other harvester ant species (Fewell, 1988; Baroni-Urbani and Nielsen, 1990; Reyes-López and Fernández-Haeger, 1999). Besides, the propensity of harvester ants to quickly exploit a food source determines their ability to monopolise it and defend it against competitors.

4.1.2. Influence of seed nature

Several studies showed preferences of harvester ants for some seed species, in particular with a view to quantifying the impact of the myrmecofauna on the plant populations' dynamics (Brown et al., 1979; Inouye et al., 1980; Davidson et al., 1985; Hobbs, 1985; Detrain and Pasteels, 2000). Our experiences with either monospecific or bispecific mix of seeds having the same size, confirm the importance of seeds' nature on the recruitment dynamics in *M. barbarus*. Indeed, the higher mobilisation rate of colonies was obtained towards the mix containing canaryseeds, which are much appreciated. This seems to result from the combined effects of a higher probability of workers to lay a trail at the beginning of the recruitment towards the bispecific mix, and of the perception of canaryseeds by workers inside the nest, eliciting a higher rate of exits. This higher foraging response to canaryseeds is not only due to the preferential harvesting of little items (as shown earlier in the discussion). Indeed, when comparing the harvesting rate of oat fragments (in monospecific mix) with that of canaryseeds (in bispecific mix), we find out that this seed is proportionally more harvested than oat fragments (Mann–Whitney test, $p=0.04$). In this respect, it is known that chemical compounds of seeds can determine the feeding preferences of ants' species. In the case of myrmecochorous plant species, seeds even develop fleshy appendages, called elaiosomes, bearing chemical cues attractive to the ants. These plants are dispersed by ants, which carry seeds into their nests, consume the elaiosomes, and discard the remaining seed afterwards (e.g. Beattie and Hughes, 2002). Similarly, several studies on harvester ant species have reported clear-cut preferences for some seed species.

However, regarding harvester ants, few succeeded in identifying the chemical compounds responsible for the attraction of workers (Nickle and Neal, 1972; Kelrick et al., 1986). In the present study, one cannot explain the preferential harvesting of canaryseeds by *M. barbarus*' colonies by differences in their nutritional composition, and hence in their expected energetic benefit. Indeed, oat and canaryseeds have quite the same proportion of proteins, carbohydrates and lipids (Matz, 1991; Abdel-Aal et al., 1997). Nevertheless, minor compounds, water content and/or seed hardness could play an important role in seed selection by harvesting workers. This would deserve a further comparative analysis of canary and oat seeds' features.

4.2. Relative participation of castes in food recruitment

Worker size is correlated with many aspects of foraging, including trail-laying, load carriage potential, activity costs, and risk susceptibility. Each worker caste is not equally armed against predation or heat shock risks: ant susceptibility to temperature is expected to decrease with worker's cuticle thickness and larger body size, while predation risks are highly variable according to the size ratio between the worker and its potential enemy.

The respective role of castes in recruitment is well known, namely in dimorphic ant species. Generally, *major* are mobilised late and only in case of intense recruitment towards large sources. There is such a polyethism that *minor* workers are specialised in the laying of the trail pheromone while *major* produce none or little trail pheromone [e.g. *Pheidole* dimorphic genus (Hölldobler and Möglich, 1980; Itzkowitz and Haley, 1983; Detrain and Pasteels, 1991)]. By contrast, in harvester ants, we show that there is not a single caste responsible for trail-laying in *M. barbarus*, insofar as this behaviour is observed in the three sizes of workers. The three *M. barbarus* castes can lay chemical trails, but those laid with *media*'s glands are followed over longer distances (Heredia and Detrain, 2000). In addition, the present study shows, for the first time in a polymorphic harvester ant, different levels of caste recruitment according to the features of available seeds. *Messor barbarus*' *media* always show higher mobilisation indexes, and are more numerous at foraging arenas than *minor* or *major*. In addition, *media*

always appear first at foraging arenas, whichever the seeds presented. These *media*, which are numerically dominant in recruitment, are primarily responsible for trail-laying. *Minor* participate in foraging as well, but mostly when they can be efficient in carrying seeds, such as in the presence of oat fragments. In this case, *minor* are quickly mobilised towards the arena and can actively participate in trail-laying showing a high probability of performing this task. At the beginning of the recruitment, the exit of *minor* could be triggered concurrently by the recruitment trail laid by the first returning *media*, and by the arrival of nestmates carrying seeds of the preferred size. The implication of this *minor* caste in the harvesting activity seems thus to depend on their success in the picking up and carrying of seeds. By contrast, the difficulty, or even the failure of picking up or carrying seeds can progressively lead a worker to disengage from this activity, as observed for *minor* in the presence of whole oat seeds. Differential mobilisation of castes can thus be related to their seed-carrying potential insofar there is a pairing of forager size and seed item size, as previously reported in other harvester ant species (e.g. Rissing and Pollock, 1984; Traniello and Beshers, 1991; Crist and MacMahon, 1991a,b, 1992; Wilby and Shachak, 2000).

Regarding *major*, they tend to show a proportionally higher mobilisation index towards the bispecific mix. As they can potentially harvest bigger seeds than the other castes, they could significantly contribute to the energetic intake, despite their small absolute number in the colony. The probability of *major* to lay a trail is always low, although a tendency for a stronger participation in this task is observed in the presence of whole oat, alone or mixed. Instead of being involved mainly in seed retrieval and in the building-up of recruitment, like *media*, these *major* could be specialised in the performance of some tasks, such as the cutting of plant twigs or could play a role in patrolling much appreciated food sources. Indeed, worker size affects not only the harvesting ability, but also the susceptibility to threats from predators or from competing ant species. *Major* workers could be effective fighters that discourage intrusion by competitors and maintain colony access to food finds. Division of labour between workers of different sizes results from a balance between the energetic gain for the colony, the need for cooperative food exploitation, and the susceptibility to predation and/or competition risks. All these parameters vary according

to the characteristics of seed patches, and expectedly increase with items size. The colony should then adjust the relative participation of each worker caste, in order to optimize the trade-offs between a quick information transfer through recruitment, most efficiently implemented by *media*, and a high energetic gain per forager, depending on worker/seed size ratio.

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