

## Research article

# A field assessment of optimal foraging in ants: trail patterns and seed retrieval by the European harvester ant *Messor barbarus*

C. Detrain, O. Tasse, M. Versaen and J.M. Pasteels

Laboratoire de biologie animale et cellulaire CP. 160/12, Université Libre de Bruxelles, Avenue F. Roosevelt 50, B-1050 Bruxelles, Belgium,  
e-mail: cdetrain@ulb.ac.be; jmpasteel@ulb.ac.be

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**Summary.** The ant *Messor barbarus* is a major seed predator on annual grasslands of the Mediterranean area. This paper is an attempt to relate the foraging ecology of this species to resource availability and to address several predictions of optimal foraging theory under natural conditions of seed harvesting.

Spatial patterns of foraging trails tended to maximise acquisition of food resources, as trails led the ants to areas where seeds were more abundant locally. Moreover, harvesting activity concentrated on highly frequented trails, on which seeds were brought into the nest in larger numbers and more efficiently, at a higher mean rate per worker.

The predictions of optimal foraging theory that ants should be more selective in both more resource-rich and more distant patches were tested in the native seed background. We confirm that selectivity of ants is positively related to trail length and thus to distance from the nest of foraged seeds. Conversely, we fail to find a consistent relationship between selectivity and density or species diversity of seed patches. We discuss how selectivity assessed at the colony level may depend on factors other than hitherto reported behavioural changes in seed choice by individual foragers.

**Key words:** Optimal foraging, harvester ants, trail, distance, seed abundance.

## Introduction

Optimal foraging theory was initially developed from studies on vertebrates (see e.g., Maynard Smith, 1978; Krebs and Davies, 1992) and was extended to encompass social insects that carry food items back to a central place where food is eaten or stored (Orians and Pearson, 1979). Correspondence between predictions of this theory and foraging behaviour in social insects has been investigated in bumblebees (see e.g.,

Pyke, 1978; Cartar and Dill, 1990; Harder, 1990; Waddington, 1995), honeybees (see e.g., Schmid-Hempel et al., 1985; Schmid-Hempel and Schmid-Hempel, 1987) and ants (see e.g., Traniello et al., 1984; Holder Bailey and Polis, 1987; Fewell, 1988; Crist and MacMahon, 1991; Ferster and Traniello, 1995; Fewell et al., 1996). Optimality models have recently been challenged by observations of “sub-optimal” performance at the individual level, in bees (Nunez, 1982) and ants (Kacelnik, 1993; Rocés and Nunez, 1993; Detrain et al., 1999). These latter studies suggest that, in eusocial insects, foraging strategies are a trade-off between individual efficiency of food retrieval and information transfer to nestmates through recruitment.

In other respects, the match between optimal foraging theory and feeding behaviour of foragers remains controversial. For instance, the expected increase in feeding selectivity as a function of distance to a forage site has not been unanimously validated in ants. On the one hand, increasing selection with distance was confirmed in *Pogonomyrmex barbatus* (Davidson, 1978) and also in *P. occidentalis*, although outside its normal foraging range (Crist and MacMahon, 1992). On the other hand, similar experiments on harvester (see e.g., Rissing and Pollock, 1984; Holder Bailey and Polis, 1987; Baroni-Urbani and Nielsen, 1990; Ferster and Traniello, 1995) or leaf-cutting ants (see e.g., Wetterer, 1991) failed to show any significant change in the size range of food items collected at different foraging distances.

Most of these studies testing optimal foraging theory in ants were focused on harvester species living in North American desert and semi-arid environments. Experiments were carried out either in the laboratory or in semi-natural conditions by using baits of non-native seeds (but see Crist and MacMahon, 1992). While artificial baits allow the control of food availability, reality was somewhat distorted in these oversimplified environments. The present study is an attempt to relate the concept of optimal foraging to the harvesting behaviour of a European ant, *Messor barbarus*,

under natural conditions of seed availability. Presumably, ant colonies are able to maximise acquisition of resources both by fitting the spatial distribution of foragers with that of food items and by adapting foraging behaviour to environmental constraints. Therefore, our main objectives are: 1) to study colony adjustments of trail networks and foraging activity in response to changes in seed availability in the biotope; 2) to examine changes in foraging selectivity of *M. barbarus* in relation to seed abundance and foraging distance.

## Methods

### Study site

The study site was located in the Southeast of France, at Vidauban (elevation ca 80 m). Natural stone plates and gravel areas separated patches of herbaceous plants. This Mediterranean grassland was characterised by a high diversity of spermatophytes (up to 78 different species). The tree cover was made up of pine trees *Pinus pinea* while *Cistus monspeliensis* and *Juniperus oxycedrus* dominated the ever-green shrub canopy. The study was conducted from April to July 1995 and from April to June 1997 during the bout of plant flowering which followed the winter rains of February and March. The ant fauna was mainly composed of *Cataglyphis cursor*, *Crematogaster scutellaris*, *Camponotus cruentatus* and *Messor barbarus*. The density of *M. barbarus* colonies was very low (four colonies/ha) and reflected a limitation of sites in which soil layers above stone plates were deep enough to house large nests of harvester ants. This loose nest spacing pattern reduced competition for resources between neighbouring colonies which is known to affect trail arrangement and foraging ecology of *M. barbarus* (Acosta et al., 1995). We chose to focus our study on a single *M. barbarus* colony, which allowed us to monitor both ant harvesting activity and local seed availability in a rectangular plot of 32 m × 40 m ungrazed by cattle. This colony was the only one present within the studied plot.

### Global and local availability of seeds

All fruiting plants found on the study site were identified to species and their seeds were preserved in a reference file. In the present paper, the term "seed" refers without distinction to whole fruits or seeds, which are retrieved by the ants. Seed availability was assessed by examining the surface seed supply and the standing crops currently growing in the colony neighbourhood. We measured the global availability of seeds to give an overview of the seed density on the study area, and the local availability of seeds to give the seed density at the end of each foraging trail.

The global seed availability of the 32 m × 40 m-study site was assessed every month by counting the number of seeds available on plants and over the soil surface in 30 samples. Each sample consisted of a circle, 314 cm<sup>2</sup> in area, centred in a 1 m<sup>2</sup> quadrat. The 30 quadrats to be sampled were chosen randomly from the possible 1280 quadrats of the whole study area.

Global seed availability provides a monthly estimate of the diversity and density of seeds available on the study site. In order to verify possible differences between this global seed abundance and the food resources actually experienced by the ants, we performed measures of local seed availability. Therefore, each time a new trail was observed, the number of seeds available over the soil surface and on the individual plants were counted in 5 circles (78 cm<sup>2</sup> each) taken within the area newly foraged by the ants. These five samples were chosen by centring a 2-m radius half-circle on the end of the new foraging trail and by taking the samples at a random distance with respect to the interval 0–200 cm, in each of the five 36° sections of the half-circle. The local seed availability associated with each foraging trail was calculated by

adding the numbers of seeds found in the 5 samples for all plant species. Data on local seed densities were not normally distributed and so were log-transformed before testing for between-months differences by means of one-way analyses of variance.

### Patterns of foraging trails and harvesting activity

The mapping of trail paths was carried out using a coordinate system by dividing the whole study site into a grid with quadrats of 1 m<sup>2</sup>. Every day, the surface around the nest entrance was carefully inspected to detect any change in the pattern of trails. This mapping was facilitated by the low grass density and by the large stone plates covering the study site. The total length, the persistence of trails as well as the number of branching points (one branching point being defined as the junction of two distinct foraging trails) were measured. Data were considered as independent since most trails occurred on distinct days or were observed several days apart (in April, up to one week apart). Moreover, a trail feature did not depend on that previously observed since successive observations were never significantly correlated. Between-months differences in these trail features were therefore tested by means of one-way analysis of variance (ANOVA) for each year of observation.

At 2 m from the nest entrance, three 2-min flow counts of loaded and unloaded ants were carried out daily between 15–17 h on each foraging trail. The averaged values of these flows provided a measure of the daily harvesting activity of the colony. The relation between the global activity of a colony and its harvesting efficiency was tested by correlating the number of incoming ants and the percentage of individuals loaded with a seed. Foraging between 15–17 h was considered as a good indicator of colony activity, since during this time trails were well established and foraging flows were maximal in both directions (from or to the nest). To check whether the 15–17 time schedule remained valid from April until the beginning of July, we performed hourly counts of forager flows once every fortnight, during a 24 h-cycle.

### Selectivity of the ant colony

The selectivity of *M. barbarus* harvesting behaviour was studied by observing items actually returned by workers to the nest. Seed retrievals were measured on each trail, 2 m from the nest entrance, by a survey and identification to species (or at least genus) of the loads of 100 incoming foragers. This sampling of 100 seeds was carried out during the peak diurnal activity. As far as possible, seeds were identified directly in the field in order to limit disturbance of ants on the trails. For unrecognized seeds, the retrieved item was taken from the worker, stored in a vial and identified under a binocular microscope.

To determine whether *M. barbarus* foragers were opportunistic or selective while harvesting native seeds, we considered how seed intake was related to local seed availability at the end of foraging trails. This allowed us to associate a measure of feeding selectivity with each observed foraging trail. The selectivity of the *M. barbarus* colony was given by the coefficient  $B_s$  (Schoener, 1974) which weighs the relative occurrence of a seed species  $i$  in the diet ( $d_i$ ) by the reciprocal of its relative environmental availability in the surroundings of the trail end ( $f_i$ ). This selectivity coefficient was defined as

$$B_s = \frac{1}{\sum_{i=1}^m (d_i/f_i)^2}$$

The selectivity value ( $B_s$  value) can be considered as an estimate of the breadth of the dietary niche which reflects the selective or generalist trend of *M. barbarus* harvesting behaviour: lower  $B_s$  values indicate high selectivity from the ants in relation to seed availability. As seed density, species diversity and foraging distance may be correlated with each other, the influence of these variables on ant selectivity was assessed by using partial correlation coefficients.

## Results

### Global and local availability of seeds

The density of seeds available globally on the study site strongly differed between 1995 and 1997 (Table 1; up to 6500 seeds/m<sup>2</sup> in 1995 versus 950 seeds/m<sup>2</sup> in 1997). Within each year, the global seed availability changed over the observation period. It increased by a factor of 9 from April to July 95 and it nearly doubled from April to June 1997. At the end of trails, local seed densities and species diversity did not significantly fluctuate in 1997 (Table 1; between-month comparisons of local seed densities  $F = 1.9$ ;  $df = 2,20$ ;  $P > 0.05$ ; of number of seed species  $F = 0.24$ ,  $df = 2,20$ ;  $P > 0.05$ ). In 1995, the local seed availability increased over months of observation in terms of both seed density and species diversity (between-months comparisons of local seed densities,  $F = 7.6$ ;  $df = 3,33$ ;  $P = 0.0005$ ; of number of seed species,  $F = 4.6$ ;  $df = 3,33$ ,  $P = 0.008$ ). This increase was, however, time-limited to the beginning of spring (with a more than 20-fold increase in local seed density between April and May 95; Table 1). Due to the high spatial heterogeneity of the study area, the global estimate of seed resources did not reflect the seed availability actually experienced by ants at a more local scale, at the end of their foraging trails. These trails always led the ants to plant patches where seeds were locally more abundant. Indeed, in both years, the local density of seeds found at the trail end always showed higher values than did the global seed availability concurrently estimated over the whole study site. Densities of seeds were twice to 38 times higher at the end of a trail than on neighbouring areas (Table 1).

### Patterns of foraging trails

*M. barbarus* workers travelled on well-defined trails, since vegetation and other obstacles found by workers on their foraging routes were cleared. Branching points were rarely observed on the trail network (Table 1; number of branching points below 1 on average). This indicates that trails were often single paths at the end of which foragers dispersed to exploit neighbouring areas. When ramified, trails were divided into 2 to 3 branches at most. In contrast to the large fluctuations of global seed densities, no significant between-month change was observed in the ramification of the trail network (Table 1; between-month comparisons of the mean number of branching points per foraging trail in 1995,  $F = 0.25$ ;  $df = 3,42$ ;  $P > 0.05$  and in 1997  $F = 1.14$ ;  $df = 2,20$ ;  $P > 0.05$ ).

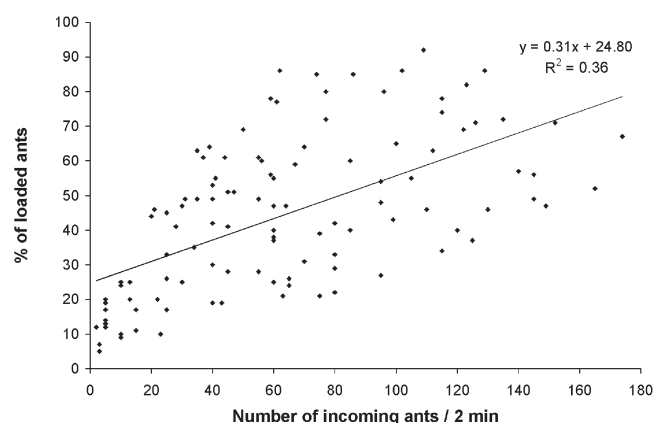
Foraging trails extended from 1 to 25 m away from the nest. Their mean length did not change significantly between months in 1995 (Table 1;  $F = 1.4$ ,  $df = 3,42$ ;  $P > 0.05$ ) or in 1997 ( $F = 0.5$ ;  $df = 2,20$ ;  $P > 0.05$ ). Each trail was followed by workers for 2.5 days on average ( $n = 46$ ,  $SD = 2.1$ ) in 1995 and 2.4 days ( $n = 23$ ,  $SD = 0.95$ ) in 1997, and between-month changes in trail persistence were not statistically significant (Table 1; in 1995,  $F = 0.62$ ;  $df = 3,42$ ;  $P > 0.05$  and in 1997,  $F = 0.46$ ;  $df = 2,20$ ;  $P > 0.05$ ).

### Harvesting activity of the ant colony

*Messor barbarus* harvesting activity fluctuated from one day and one trail to another. In both years of observation, the flows of ants foraging during the day reached their peak

**Table 1.** Seed availability and features of *M. barbarus* foraging trails over successive months of observation in 1995 and 1997. Mean and standard deviation are given as well as the number of trails observed (n). Local seed availabilities were averaged on all trails observed during a one-month period

Variables		Month – Year				Month – Year		
		April 95	May 95	June 95	July 95	April 97	May 97	June 97
<i>Seed availability</i>								
Global density on site n seeds × 10 <sup>3</sup> /m <sup>2</sup>		0.69	2.36	3.62	6.50	0.51	0.78	0.95
Local density at trail end n seeds × 10 <sup>3</sup> /m <sup>2</sup>	Mean	3.90	89.85	58.12	47.35	1.22	4.73	4.60
	S.D (n)	2.16 (2)	66.63 (4)	52.54 (22)	32.67 (9)	0.54 (3)	4.06 (8)	2.01 (12)
Seed species at trail end n species	Mean	2	8.7	7.45	5.2	4.0	5.4	6.7
	S.D. (n)	0 (2)	1.9 (4)	2.81 (22)	2.1 (9)	0.97 (3)	2.29 (8)	1.49 (12)
<i>Trail features</i>								
Branching points	Mean	0.3	0.1	0.3	0.2	0.3	0.5	0.75
	S.D (n)	0.6 (3)	0.3 (10)	0.7 (24)	0.7 (9)	0.6 (3)	0.5 (8)	0.45 (12)
Trail length m	Mean	13.3	8.4	14.0	11.5	16.3	13.3	15
	S.D. (n)	2.95 (3)	5.7 (10)	8.3 (24)	7.7 (9)	1.5 (3)	5.6 (8)	5.1 (12)
Persistence in trail use days	Mean	1.7	2.2	2.9	2.0	2	2.4	2.6
	S.D. (n)	1.15 (3)	2.5 (10)	2.25 (24)	1.5 (9)	0 (3)	1.2 (8)	0.9 (12)



**Figure 1.** Relationship between foraging efficiency (% of incoming ants loaded with a seed) and the intensity of ant flows on trails (number of ants returning to the nest/2 min). Each point represents the averaged value of three 2-min counts. Data obtained in 1995 and 1997 were pooled in the same graph (N = 110)

values in June (up to 200 incoming foragers/2 min). Due to the temperature-dependence of ants' activities, their foraging decreased during the day in July, under conditions of high soil temperatures ( $> 25^{\circ}\text{C}$ ). As a general rule, foraging efficiency (proportion of laden ants over the total number of incoming foragers) increased as a function of the colony activity and was higher on trails heavily followed by the ants. Indeed, the percentage of ants loaded with a seed was positively and significantly correlated to that of flows of incoming ants (Fig. 1;  $r = 0.60$ ,  $n = 110$ ,  $p < 0.001$ ). Trails drawing larger numbers of foragers showed higher rates of seeds' retrieval per worker capita.

### *Changes in seed availability and selectivity in relation to foraging distance*

The local density of seeds at the end of trails remained similar whatever the trail length (Table 2; ANOVA,  $P > 0.05$  in 1995 and 1997) and was not significantly correlated with the foraging distance from the nest (Table 3; partial correlation coefficient between local seed density and distance:  $r = -0.03$  in 1995 and  $r = 0.05$  in 1997,  $P > 0.05$ ). The diversity of seed species slightly increased (Table 2) and was positively correlated with the foraging distance (Table 3) but this trend was not statistically significant.

Selectivity coefficients ( $B_s$ ) were calculated for each foraging trail and averaged for each category of trail length (Table 2). *M. barbarus* was a rather selective ant species and showed low  $B_s$  values between 0.001 and 0.022 on average.  $B_s$  coefficients significantly decreased with increasing trail length (Table 2) and were negatively correlated with foraging distance (Table 3; in 1995  $r = -0.33$ ,  $n = 31$ ,  $P < 0.05$ ; in 1997;  $r = -0.4$ ,  $n = 19$ ,  $P < 0.05$ ). In other words, at short distances ( $< 10$  m), mean  $B_s$  values (between 0.01 and 0.02) indicated that, close to the nest, the composition of ant retrievals tended to match the local seed availability (Table 2). For trails longer than 10 m, the selectivity of ants increased, with mean  $B_s$  coefficients falling under 0.007 and even showing extreme values of 0.001.

### *Changes in selectivity in relation with the availability of seeds*

By pooling all  $B_s$  values measured in each year, we determined whether the selectivity shown by the ants was related to the diversity or the density of available seeds (Table 3). In

**Table 2.** Seed densities, number of seed species (means  $\pm$  SD) available at the end of trails and  $B_s$  value (coefficient of selectivity) in relation to the foraging distance. The selectivity of the *M. barbarus* colony is given as the average (and SD) of  $B_s$  values per category of trail length. Foraging distances were arbitrarily divided into five categories according to the trail length

	Year	0–5 m	5–10 m	10–15 m	15–20 m	> 20 m	Statistical test ANOVA
Number of trails observed	1995	4	12	7	8	4	
	1997	0	5	10	6	2	
Local seed density $n \text{ seeds} \times 10^3/\text{m}^2$	1995	53.32 ( $\pm 69.64$ )	41.91 ( $\pm 28.90$ )	53.34 ( $\pm 29.90$ )	88.21 ( $\pm 94.50$ )	56.48 ( $\pm 51.96$ )	F = 0.8 NS
	1997	–	4.04 ( $\pm 4.34$ )	4.44 ( $\pm 1.80$ )	3.93 ( $\pm 3.31$ )	4.23 ( $\pm 5.54$ )	F = 0.76 NS
Number of seed species	1995	4 ( $\pm 0.82$ )	6.8 ( $\pm 3.5$ )	7.1 ( $\pm 2.8$ )	8 ( $\pm 3.1$ )	7.5 ( $\pm 1.7$ )	F = 1.3 NS
	1997	–	4.0 ( $\pm 1.0$ )	6.1 ( $\pm 1.6$ )	6.3 ( $\pm 1.4$ )	6.5 ( $\pm 3.5$ )	F = 2.5 NS
Selectivity $B_s$ value	1995	0.022 ( $\pm 0.013$ )	0.019 ( $\pm 0.009$ )	0.007 ( $\pm 0.006$ )	0.001 ( $\pm 0.001$ )	0.003 ( $\pm 0.002$ )	F = 2.8 P = 0.04
	1997	–	0.011 ( $\pm 0.012$ )	0.004 ( $\pm 0.003$ )	0.0025 ( $\pm 0.004$ )	0.002 ( $\pm 0.004$ )	F = 2.9 P = 0.05



**Table 3.** Partial correlation coefficients between variables for each year of observation. Levels of significance are given for each correlation coefficients (NS =  $P > 0.05$ ). Selectivity of *M. barbarus* is given by the Bs value associated with a foraging trail (a lower Bs value accounts for a higher ants selectivity), seed density = local density of seeds available at the end of trail (Ln transformed values for normality), n seed species = number of seed species locally available at the trail end, Distance = length of the foraging trail

Variable comparison	Year 1995			Year 1997		
	r	N	P	r	N	P
Distance $\times$ seed density	-0.03	31	NS	0.05	19	NS
Distance $\times$ n seed species	0.23	31	NS	0.10	19	NS
Bs value $\times$ distance	-0.33	31	$P = 0.03$	-0.40	19	$P = 0.04$
Bs value $\times$ seed density	-0.09	31	NS	-0.17	19	NS
Bs value $\times$ n seed species	-0.08	31	NS	-0.56	19	$P = 0.004$
Seed density $\times$ n seed species	0.41	31	$P = 0.02$	0.02	19	NS

both 1995 and 1997 years, we failed to find any significant relationship between selectivity and seed density. Conversely, the ants' selectivity was significantly related to the diversity (number) of seed species available at the end of trails in 1997 (Table 3, partial correlation coefficient between Bs values and local seed diversity:  $r = -0.56$ ,  $n = 19$ ,  $p < 0.01$ ). This latter trend was not confirmed by data from the 1995 year.

## Discussion

Foraging strategies in insect societies are assumed to be evolutionary responses that seek to maximise collective efficiency in food retrieval. Based on this assumption, each ant colony should allocate foragers and, therefore invest energy (and time) among different feeding sites in order to harvest food in the most efficient way. Patterns of foraging trails in ants are amongst the most striking examples of behavioural adaptations to the availability of food resources. For instance, the swarm patterns of army ants are known to change according to prey density (Deneubourg et al., 1989; Franks et al., 1991). Similarly, trail patterns of harvester ants are influenced by food abundance (e.g., Bernstein, 1975; Rissing and Wheeler, 1976; Hölldobler, 1976; Goss and Deneubourg, 1989; Gordon, 1991). In *Messor barbarus*, shorter trunk-routes and enhanced branching of the trail network were found in conditions of richer seed availability (Lopez et al., 1993, 1994a, b). This trend was shown on two different scales of analysis as a response to yearly fluctuations in resource abundance or to biotope differences in vegetation density. In the present study, no such major structural changes were detected in response to monthly and even yearly changes in seed densities. At our spatial scale of analysis, within-biotope fluctuations in plant densities might be too small to alter significantly the global features of the trail network. Our data nevertheless demonstrate that the network of *M. barbarus* trails is a flexible structure related to the seed pool abundance. Indeed, the distribution of seed patches influenced the spatial orientation of *M. barbarus* trails, as

each foraging trail ended in areas showing higher densities of seeds. Selection of the most valuable seed patches at the colony level probably resulted from higher rates of trail reinforcements by individual foragers coming back from resource-rich areas.

As for the spatial orientation of trails, the foraging activity on these trails is closely related to nutrient availability. Higher number of foraging ants often coincide with greater density of seeds as highlighted in *Pheidole* (Whitford et al., 1980), *Messor structor* (= *rufitarsis*) (Hahn and Maschwitz, 1985) and *Pogonomyrmex* spp. (Hölldobler, 1976; Davidson, 1977; Crist and MacMahon, 1992). In addition, on highly frequented trails of *M. barbarus*, seeds are brought into the nest not only in larger numbers, but more efficiently with a higher mean rate per worker. Since not all *M. barbarus* ants walking on trails are foragers but may be specialised in patrolling or defence of the nest surroundings, a higher proportion of foragers mobilised on frequented trails may explain the perceived increase in foraging efficiency. Where seed production is irregular, this may allow the colony to respond to short-term changes by concentrating its harvesting effort on resource-rich areas, while the storage of seeds in granaries creates a buffer between the colony and its environment.

Trends in selectivity of *M. barbarus* may also be discussed in view of basic qualitative predictions of optimal foraging theory which have been questioned for several harvester ant species since the expected tendencies were not always detected (see, e.g., Rissing and Pollock, 1984; Holder Bailey and Polis, 1987; Crist and MacMahon, 1991; Ferster and Traniello, 1995).

Correspondence of our field observations with the theoretical prediction that ants would become more selective with the increase of foraging distance is notable. Indeed, *M. barbarus* selectivity significantly increased with longer travel distances. Such a trend was previously reported in *P. occidentalis* but only occurred outside its normal foraging range (Crist and MacMahon, 1992). *M. barbarus* foraging in the native seed background also corroborate data from feeding experiments using artificial baits and carried out on

*Pogonomyrmex barbatus* (Davidson, 1978). This behavioural trend of *M. barbarus* fits predictions of the central-place foraging theory (Orians and Pearson, 1979; Schoener, 1979), where workers engaged in a long foraging journey are expected to be more selective at the seed patch in order to optimise their energy/time investment. Since the cost of walking per unit time is much lower than the seed energetic reward, time investments could have a prevailing influence on seed choice and load transport strategy in harvester ants (Fewell, 1988; Morehead and Feener, 1998; Ratnieks and Anderson, 1999; Reyes and Haeger, 1999). Behavioural changes may thus occur in *M. barbarus* foragers, which become more discriminating in their seed choices as the foraging distance increases. However, we currently lack evidence that *M. barbarus* ants really collect the most energetic and/or easier seeds to carry at long distances (Detrain et al., 1996; Detrain and Pasteels, 1999). The increase in selectivity with distance may indirectly result from the interplay between trail evaporation and some modulation of recruitment mostly by *M. barbarus* medias (Heredia et al. 1999), which may lay larger amounts of trail pheromone when returning from patches of preferred seed species. Since trail evaporation limits foraging at long distances, only intense chemical marking by ants harvesting on their preferred seeds will allow the emergence as well as the maintenance of a trail leading to remote areas. An alternative explanation exists that does not assume distance-dependent changes in decision-making and seed choice by ants. Actually, enhanced selectivity with distance might be a by-product of an uneven distribution of seed species in which the pool of preferred seed species might be available only in remote food patches and might be depleted close to the nest. Indeed, even when ants consume only a small percentage (less than 10 %) of the total seed production at a site, the concentration of their foraging activity on some preferred plant species can result in local impoverishment in these seed species in the nest neighbourhood (Tevis, 1958; Rogers, 1974; Reichman, 1979; Inouye et al., 1980; Gillon et al., 1984; Hobbs, 1985).

Another prediction of the theory that ants would become more selective with increasing availability of food resources was not confirmed by our field observations. Feeding selectivity of *M. barbarus* was independent of density of native seeds. This result contrasts with increased dietary specialisation observed at sites of high food abundance for *Aphaenogaster* (formerly *Novomessor*) *cockerelli*, *Messor* (formerly *Veromessor*) *pergandei* (Byron et al., 1980) and *Pogonomyrmex* species (Davidson, 1978; Whitford, 1978). However, some of these experiments need to be interpreted with caution since densities of seeds offered at artificial baits were always lower than those observed in natural conditions. Therefore, the decreasing selectivity of *P. barbatus* (Davidson, 1978) at low-density seed baits may result from a significant decrease over time in encounter rates of ants with preferred seeds and does not necessarily imply a change in their behaviour. As regards the diversity of seed species, it was significantly related to the feeding selectivity of *M. barbarus* only in the year 1997. Foraging preferences, which may limit the number of species harvested by the ants, could explain

why higher selectivities are often associated with conditions of higher availability of seed species in 1997. This trend however lacks consistency since, in 1995, feeding selectivity did not seem to be altered by the number of species of available seeds.

Some, but not all data presented here give qualitative support for optimal foraging predictions. Further work is however needed to understand how ants might shape their behaviour in order to forage optimally and how amplification processes (e.g., trail recruitment) or environmental features might contribute to the emergence of adaptive foraging strategies.

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