Food Storage in the Nest and Seed Selectivity in the Harvester Ant *Messor barbarus*.

by

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ABSTRACT

The degree of seed storage saturation in a *Messor barbarus* nest is a crucial factor in the foraging process, and modifies seed selection criteria. Laboratory experiments with artificial colonies of this species have shown that at low food storage levels ants are highly selective, preferring seeds of greater mass. However, saturated colonies transport hardly any seeds into the nest, and even invert selection criteria, taking seeds of lower mass. This behavior may be modified by differences in the abundance of each of the seed species concerned.

Keywords: Harvester ants, Seed preferences, Seed size, Foraging

INTRODUCTION

The process of selection, by a harvester ant colony, of the types of seed to be used as food is currently considered highly complex, and is influenced by numerous factors (MacMahon *et al.*, 2000). These include the size of available seeds (Davidson, 1978), their abundance or relative density (Crist & MacMahon, 1992, Kunin 1994), smell (Warburg 2000), chemical properties (Gordon 1980), the presence of endophytic and saprophytic fungi on seeds (Crist & Friese 1993), temporal patterns of availability (Mehlhop & Scott 1983), and even competition with other species (Andersen *et al.*, 2000). It is very likely that additional factors are involved.

In *Messor*, the predominant harvester-ant genus in the Old World, seed mass appears to exert considerable influence on the selection process. It is reported, for example, that seed selection is directly proportional to seed mass in *M. bouvieri* Bondroit and *M. barbarus* (L.) (Detrain & Pasteels 2000, Willot *et al.*, 2000), very small seeds being rejected, although not invariably (Cerdan *et al.*, 1986). In other species, such as *M. galla* (Mayr), a more opportunist selection system appears to predominate, using the seeds most common in the vicinity (Gillon *et al.*, 1984).

One of the most striking features of harvester ants is their ability to

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store large amounts of seed within the nest. The mass of stored seeds is related to the number of workers and larvae in the colony (Gentry 1974). This "granary" works to reduce dependence on the outside world, by serving as a buffer. The colony is thereby enabled to cope with momentarily unfavorable situations (e.g. adverse weather or increased predation rates) by reducing outdoor activity. Indeed, defence against predators is one hypothesis put forward (MacKay & MacKay 1984) to account for the appearance of within-nest storage capacity. Moreover, these are not static reserves; their composition can vary as a result of indoor consumption and outdoor availability, and some species may even be removed in order to make way for others (MacMahon *et al.* 2000).

Thus, given the importance of these seed stores to the biology of harvester ants, they may represent an additional element in the seed selection process. The main aim of this study was to determine whether the amount of food stored by the colony affected seed selection.

MATERIAL AND METHODS

The study used four 2-year-old *M. barbarus* colonies, developed in captivity from founding queens, and comprising an average of roughly 120 workers, no larvae, and only a few hibernating eggs (the usual status of a colony of this age at the start of Spring, Cerdan & Délye 1987).

The artificial nest consisted of three linked plastic boxes. Two of these served as an "indoor area" of 14 x 8 x 3 cm, with an opaque cover and the other as an open-topped "foraging area" of 30 x 20 x 15 cm. A mineral oil barrier prevented ants from escaping.

Three types of experiment were performed:

Experiment 1

Colonies were offered a mixture of seeds from nine herbaceous species (see Table I); 1 g of each species (total 9 g) was placed in a Petri dish in the "foraging area". The seed mixture was kept inside the area for 48 hours, until it was clear that ants had stopped transporting seeds. Food reserves had previously been removed from nests, so those granaries were empty when ants were gathering. Finally, the amount of each seed species rejected by the ants was determined.

Experiment 2

One week after the first experiment, the same amount of the same seed mixture was offered to the ants. In this experiment, however, granaries were not previously emptied, and were in fact almost full (roughly 8 g of seeds).

Experiment 3

The experimental design was identical to the previous one, but seed

Table 1. List of seeds used in experiments with *M. barbarus*. Mean seed weight (mg) of each species is shown in the last column (MSW).

SPP	Family	MSW (mg)
1. *Trifolium subterranea*	Leguminosae	5.670
2. *Medicago polymorpha*	Leguminosae	3.840
3. *Avena barbata*	Gramineae	2.800
4. *Erodium cicutarium*	Geraniaceae	1.780
5. *Phalaris aquatica*	Gramineae	1.230
6. *Trifolium campestre*	Leguminosae	0.190
7. *Leontodon tuberosum*	Compositae	0.053
8. *Poa annua*	Gramineae	0.023
9. *Diplotaxis catholica*	Cruciferae	0.016

availabilities were modified: the amount of seed corresponding to the 3 species with the smallest seeds was doubled (2 g) (Table 1). The same colonies were used, one week after experiment II, having again emptied the granaries.

All seeds were taken from the excavation of natural *M. barbarus* nests, and therefore some species had been modified by the ants (e.g. the pappus had been removed from *Leontodon* seeds). Only those species present in granaries in amounts sufficient to enable the experiment to be performed were selected for experimental purposes.

RESULTS

In Experiment 1, ants gathered between 84.75 % and 92.41 % of the seeds available. Almost all the available *T. subterranea*, *A. barbata* and *P. aquatica* seeds were gathered (Fig. 1); seed mass in all three species is large. *L. tuberosum* was the most frequently-encountered species in the ungathered seeds (accounting for up to 52% of the total). A close inverse correlation was found (r_S=-0.698 $p<0.001$ n=36) between mean seed mass and percentage presence in ungathered remains (seeds not transported into the nest): the greater the seed mass, the smaller the percentage presence in ungathered remains.

In Experiment 2, workers gathered only 18.78 - 28.17 % of seeds, abandoning the rest. A positive correlation was detected between seed mass and percentage presence in ungathered remains (r=0.383 p=0.021 n=36); i.e. ants opted to transport the smallest seeds, but in very small quantities. Differences in selection rates between species were negligible. In Experiment I the coefficient of variation between species for percentage presence in ungathered remains was very high (CV: 144 - 166.6), while in Experiment II this coefficient declined considerably

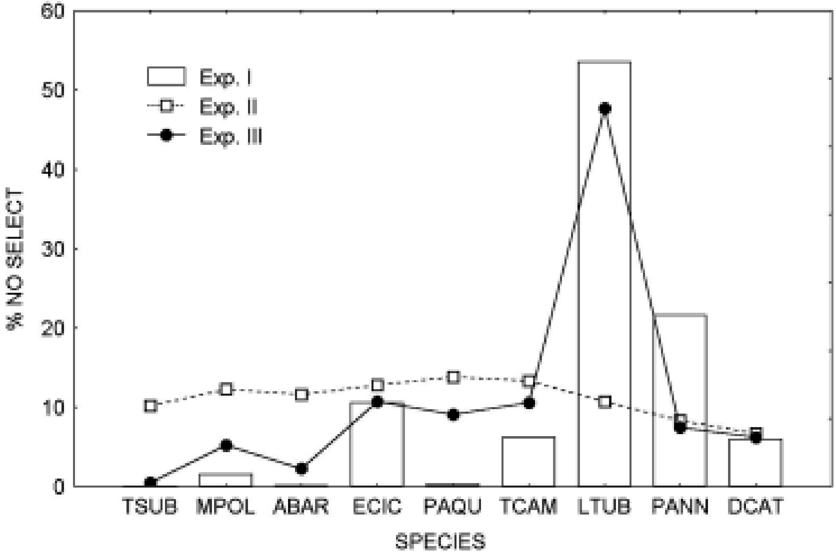

Fig. 1. Percentage of seeds selected by ants in the three laboratory experiments. Species are ordered by mean seed weight.

(CV: 19.2 - 29.9), since the percentage presence of the various species in ungathered remains was very similar (Fig. 1).

In Experiment 3, where seed stores were empty and the proportion of small seeds was increased, results were similar to those obtained in Experiment 1. Ants gathered 88.63 – 92.62 % of available seeds. The correlation between seed mass and selection rate was slightly lower than in Experiment I (r_S=-0.467 p=0.004 n=36). This difference is due to a modest increase in the amount of LTUB, PANN and DCAT seeds gathered (Fig. 1). Similar amounts of the most widely-selected species from Experiment 1 were gathered in Experiment 3 (Fig. 1); therefore, since the overall amounts transported were similar, there must have been a decrease in amounts transported for intermediate species (PAQU and TCAM).

Correlation between the four colonies was very high in Experiments 1 and 3, with r_S values between pairs of colonies ranging from 0.919 to 0.987. In Experiment 2, a more disparate result was observed (r_S between 0.189 and 0.902)

DISCUSSION

The results obtained here indicate qualitative and quantitative differences in *M. barbarus* seed-selection criteria depending on the amount of seeds stored in the nest. When granaries were empty, colonies transported a large amount of seeds; the amount transported was directly proportional to seed mass (Experiment 1). When granaries were full, the opposite trend was observed: fewer seeds were transported, and ants were less selective, although small seeds predominated (Experiment 2). The relative proportions of available seeds (Experiment 3) may modify selection, even when seeds previously selected by ants are offered (i.e. seeds taken from within natural nests).

This finding has been reported for other species of the genus, such as *M. bouvieri*, which is abundant in semi-arid areas in the south of the Iberian Peninsula (Willott *et al.* 2000). In this species, as much as 63 % of variation in seed selection can be accounted for by seed size (43 %) and relative abundance in the area (20 %). Such a strong correlation between selection and seed size has not previously been reported for *M. barbarus*, although they have been reported to reject smaller seeds of less than 0.4 mg , preferring seeds of 4-50 mg (Detrain *et al.* 2000). However, size-based selection may be modified by relative abundance. It should be remembered that seeds are not simultaneously available to the ants at all times (as is the case with the experiments performed here), since all species display an (annual) seasonal distribution.

It would therefore appear that the colony's food reserve levels influence selection criteria. If the colony's requirements are not covered (particularly if larvae numbers increase), ants select the largest available seeds, thus enabling optimization of gathering strategies, since ants obtain more calories for each foray. This selection criterion is modified by the relative abundance of the various seed species available. However, this criterion is less clear when food reserved are plentiful. Firstly, ants gather very few seeds, since foraging ceases when the granaries are full (Whitford & Ettershank 1975); secondly, and somewhat surprisingly, ants seem to prefer the smaller sizes (suggesting "laziness" on the part of the foragers).

In short, a colony's granary levels may modify food-selection criteria. This supports the view that the selection process in an ant colony is complex and multifactorial.

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