Composition-Dependent & Density-Dependent Seed Removal Rates in the Harvester Ant *Messor barbarus*.

by

Reyes-López, J. L. & J. Fernández-Haeger[1]

ABSTRACT

This study evaluated the effect of relative density and composition of locally-available seed species on selection criteria in the harvester ant *M. barbarus*. The study method was based on the use of cafeteria-style feeding experiments. Results suggest that this species tends to gather the most plentiful seeds, although selection may be modified by other factors such as seed mass. General bait composition, or "seed environment" also proved to be a major factor in selection: gathering-rates increased in the presence of strongly-preferred seeds, an increase observed even in the case of "rare" or low-density seeds. All this enables evaluation of the effect of this species on the plant community.

KEY WORDS: foraging, seed preferences, seed environment, seed density, seed size

INTRODUCTION

Ants are important seed predators in arid and semi-arid areas (Davidson *et al.* 1985; Detrain & Pasteels, 2000). Like many predators, ants select seeds (prey) for consumption from among those available at any given moment. The factors governing seed selectivity are highly complex. One of the major factors identified to date is the abundance or availability of seeds in the environment. Ants generally seem to prefer seeds which have recently matured and fallen (Briese & Macauley 1981, Briese 1982); conversely, their effect on the soil seed bank is negligible. Of the overall available species, gathering efforts focus on the most abundant species (or at least on some of them). The selection process is also dictated by the mass of each seed (directly related to its energy value); this factor, together with abundance, accounts for as much as 63 % of the variability observed in ant preferences (Willot *et al.* 2000). In other words, there is a general tendency towards gathering the most abundant and/or largest seeds.

However, seeds are not found in isolation on the ground. In many plant species, seed production is concentrated at certain times of year. On Mediterranean grassland in the southern Iberian Peninsula, the

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[1]Área de Ecología. Facultad de Ciencias. Universidad de Córdoba.Cámpus de Rabanales. Colonia de San José, 3.14071-Córdoba. SPAIN e-mail addresses:joaquin@uco.es

seeds of most annual pterophytes mature shortly after the end of the rainy season, usually in May and June. Harvester ants are most active at this is the time of year. Moreover, seeds tend to fall close to the source plants, thus giving rise to large soil seed concentrations (Harper 1977). This, together with the heterogeneous spatial distribution of the source plants, leads to the occurrence of soil patches displaying differing seed composition, in terms of both quantity and quality. This "seed environment" may influence selection by ants (Risch & Carroll 1986). Results obtained to date in studies addressing harvester-ant seed selectivity are based on the experimental provision of only two-seed mixtures.

   The aim of this study was to analyze the effects of variations in the relative abundance of different seed combinations of differing size, shape and palatability on gathering strategies in the harvester ant *Messor barbarus*.

METHODS

   M. barbarus is a very common harvester ant in grassland and cropland in the southern Iberian Peninsula. Nests are deep, with an extensive network of tunnels and side-chambers (Cerdan 1989), many of which are used for seed storage. Workers are highly polymorphic (body mass range: 0.8-40 mg) and are able to transport very large seeds (up to 248.8 mg, unpublished data). Another feature peculiar to this species is the building and maintenance of an extensive and highly-complex system of foraging-trails, which may be up to 10-12 m in length, with numerous ramifications (Reyes-López, 1986).

   The experiments described below used 10 randomly-selected *M. barbarus* nests on the University of Córdoba campus (Rabanales, Córdoba, Spain). The various seed combinations were placed around different nests depending on the degree of activity displayed over the study period. Prior to the start of the experiment, varying amounts of the study seeds were placed around nests in order to accustom the ants to these seed types.

   The study method consisted essentially in placing at the ants' disposal a constant weight (50 g) of commercial seeds, under varying experimental conditions (Table 1). This type of experiment is based on the relative mass of each seed, rather than on the number of seeds, and represents an attempt at more realistic simulation of naturally-occurring conditions (Harper 1977, Risch & Carroll 1986). Manipulation of the proportion or composition of experimental seed baits when using naturally-occurring nests is only feasible if "non-native" seeds are used; use of native species leads to interactions with the specific seed densities in the vicinity of each nest. Two types of bait were used, both

Table 1. Commercial seed species used in cafeteria-style feeding experiments, and proportion of each seed species in the two experimental mixtures employed.

Common names	Scientific names	Mass (mg)	Abbrev.	HP mixture	LP mixture
Birdseed – Alpiste	*Phalaris canariensis*	0.09	PCAN	X	X
Millet – Mijo	*Panicum miliaceum*	0.08	PMIL	X	X
Nigerseed – Negrillo	*Guizotia abyssinica*	0.05	GABY	X	X
Radish seeds – Rabanito	*Raphanus sativus*	0.14	RSAT		X
Rapeseed - Nabina, Colza	*Brassica napus*	0.06	BNAP		X
Prairie grass – Triguillo	*Bromus catharticus*	0.79	BCAT	X	
Rice – Arroz	*Oryza spp*	0.38	OSPP	X	

comprising a mixture of five out of a total of seven available commercial species (see Table 1). Both bait types included three common species (*Phalaris canariensis, Guizotia abisinica* and *Panicum miliaceum*) and two specific species: in type 1 bait, *Bromus catharticus* and *Oryza spp* were included as high-preference seeds, while in type 2 bait these were replaced by *Brassica napus* and *Raphanus sativus* as low-preference seeds. For the present study, seeds were regarded as "low-preference" if ants experienced difficulty in handling them due to spherical shape, very smooth cuticle and absence of external grippable appendices (although other factors were not ruled out). Classification of seeds as high-preference or low-preference was based on the results of previous experiments. The 50-gram seed baits were placed in a Petri dish of 14 cm. diameter (with a lateral opening to facilitate ant access) positioned 1 m from nest entrances, beside the currently-active trail. All dishes were exposed for a constant 30-minute period, since in the absence of any time limit the ants would eventually transport all the seeds to their nests and it would thus be impossible to draw conclusions regarding foraging preferences. Several days prior to the start of the experiment, similar baits were placed in the vicinity of nests, in order to accustom ants and obtain a faster gathering-response.

Two seed-mass proportions were established for each type of bait: for control purposes, the dish contained exactly 10 grams of each of the five seed species (Initial Mass 10 g: IM-10); for experiments, each species outnumbered the others by a ratio of 6:1 (30g: IM-30 versus 5g: IM-5). Thus, ants were exposed to each species in three situations:

a) With the same mass as the other species (IM = 10g);
b) As the dominant species (IM = 30g)
c) At very low mass (IM = 5g), with regard to the dominant species.

Ten dishes were placed per day (5 with a ratio of 1:1 and 5 with a ratio of 6:1) in the vicinity of nests showing activity on that day. The same

proportions were employed for both types of mixture (i.e. with high-preference and low-preference seeds). Each combination was offered twice, giving a total of 40 replicates, distributed over an average of 4 dishes/nest. Experiments took place over 4 successive days in May, 2001.

Back in the laboratory, seeds were separated and the removed mass by ants (RM) was determined. Ranks were assigned to the removed mass (variable RANK): 1 to the most-harvested species and 5 to the least-harvested. The seed removal ratio was also determined (SRR = 100 RM x IM^{-1}).

Data analysis using a multifactorial ANOVA including factors such as seed species, mixture employed or initial seed mass was not viable. When testing the assumptions for this type of analysis, very strong correlations were found between the means for the dependent variables with regard to the respective measure of variability (selecting standard deviations, variances, or standard errors), across the between-groups cells of the design (means correlated with variability). Consequently, the confidence limits of the respective means would be very high, while the overall ANOVA result would make those means appear more reliable, leading to statistically significant results. The usual transformations (such as log transformation) failed to solve this problem. Non-parametric tests were therefore used.

RESULTS

When seeds were offered in differing proportions (6:1), the average removal rank for the most abundant species (30g) was RANK=1.00 ($\pm$ 0 SD), whilst for minority species (5g) in the same mixture the average value was 3.50 ($\pm$ 1.09 SD). A value of RANK=1 implies that this was the species removed and transported to the nest in the greatest numbers in the time available (30 minutes). For all the seed species used, the mean RANK value was higher for minority species than for the most abundant species (Wilcoxon Matched Pairs Test, $p<0.05$; see Fig. 1), suggesting that ants concentrate on gathering the most abundant seeds. Similar differences were observed for seed removal ratios (SRR, Wilcoxon Matched Pairs Test, $p<0.05$; see Fig. 2): average SRR values of 78.45 % ($\pm$ 16.49 %) were recorded for the most abundant species, compared to 71.28 % ($\pm$ 20.16 %) for the minority species. This indicates that ants removed a significantly larger proportion (Wilcoxon Matched Pairs Test, $p<0.05$) of the most abundant seed species, regardless of whether the species was high-preference or low-preference. Correlations between mean SRR values for each of the seven species – as either dominant (30g) or minority (5g) species – were non-significant ($r = 0.350$ $p = 0.442$ $n = 7$).
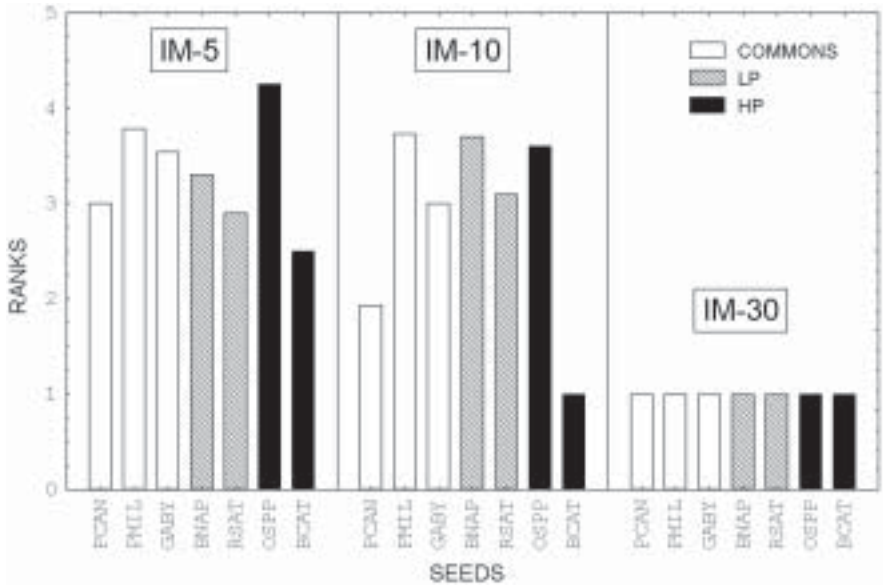
Fig. 1. Average removal ranks for the seed species used in the experiments. The most commonly-removed seed species (in mg) was assigned a value of RANK=1. Abbreviations in italics indicate species present in the two experimental mixtures.
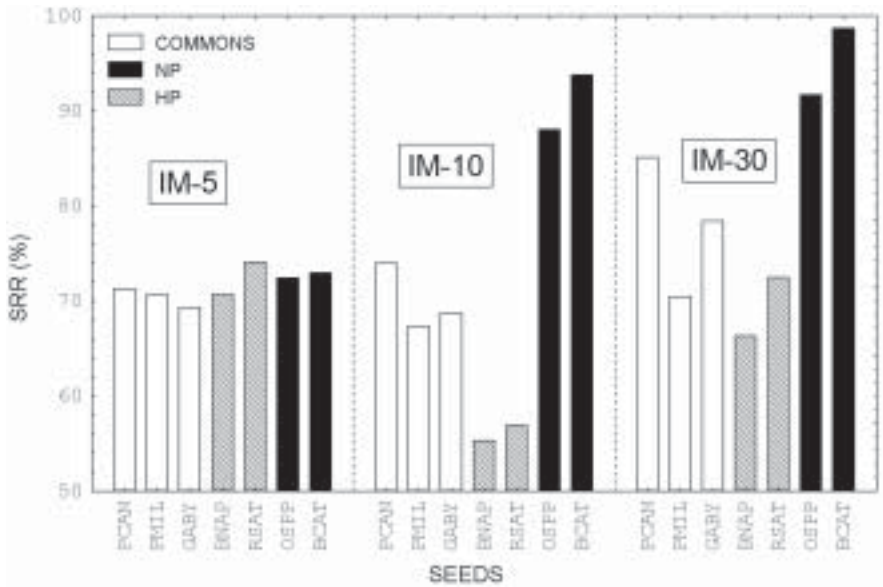

Fig. 2. Average removal rates for the seed species used in the experiments. Abbreviations in italics indicate the species common to both experimental mixtures.

Comparison of data obtained for each of seed species when dominant in the mixture (IM-30) with controls (IM-10) revealed significant differences both for the variable RANK (Wilcoxon Matched Pairs Test, p<0.05, see Fig. 1) and for SRR (Wilcoxon Matched Pairs Test, p<0.05, see Fig. 2). Mean RNK and SSR values for IM-10 were 3.00 (±1.41) and 69.11 % (± 27.57 %), respectively. Thus, the abundance of a given species with regard to the rest (1:1 ó 6:1) determined the quantity and proportion of seeds removed. The most abundant seed species was always the most frequently-removed (RANK=1).

Differences between species under IM-5 and IM-10 conditions were also significant, in terms of both RANK (Wilcoxon Matched Pairs Test, p<0.05, see Fig. 1) and SSR (Wilcoxon Matched Pairs Test, p<0.05, see Fig. 2).

A very strong linear correlation (r=0.958 p=0.001 n=7) was found between mean SSR values for each species when it was the most abundant (30 g) with respect to controls (10 g). The linear regression equation was (SRR for IM-30) = 24.211 + 0.781 (SRR for IM-10). Thus, at a ratio of 6:1 the amount of a given species removed is roughly 24% greater than at a ratio of 1:1, over the same time interval. Therefore, the superabundance of a given species in the environment triggers greater harvesting activity.

However, not all seed species elicited the same response. A strong correlation existed between seed removal rate for each species at each of the initial amounts offered (30g, 10g ó 5g) and mean seed mass (see Table 1), in equal conditions of abundance (IM-10, r=0.829 p=0.021 n=7) or superabundance (IM-30, r=0.818 p=0.027); however, this correlation disappeared when the species was in the minority (IM-5, r=0.420 p=0.348). In other words, there was a selection preference for seeds of greater mass, which disappeared when the seed species was "rare" (IM-5).

Mean values for the three common seed species in the two mixtures are summarized in Table 2. Overall comparison of SRR only for these species (in both high-preference and low-preference mixtures) yielded barely significant differences (Kruskal-Wallis test n= 96 p=0.077). However, differences between common species were greater for IM-10 (Kruskal-Wallis test n=45 p<0.001) and non-significant for both IM-30 (K-W test n=11 p=0.221) and IM-5 (K-W test n=40 p=0.244). Individual species comparisons were significant only for IM-10 (in all three cases). This means that the presence of high-preference seeds prompted a higher removal rate (both of the preferred species and of accompanying species); however, this reaction diminished with changes in the ratio of available seeds.

Table 2. Average seed removal rate (SRR) for each species in the two experimental "seed environments".

SRR (%)	LP Mixture		HP Mixture	
	Means	SD	Means	SD
PCAN	71.85	24.88	79.65	16.91
PMIL	65.85	27.27	76.30	20.28
GABY	66.37	26.91	78.58	18.20
All common seeds	68.02	26.11	78.18	17.29
RSAT	63.32	24.11	—-	—-
BNAP	66.14	23.73	—-	—-
All low-preference	64.73	23.69		
BCAT	—-	—-	82.18	12.97
OSPP	—-	—-	85.96	16.55
All high-preference			84.07	14.60

DISCUSSION

The results obtained by modifying the proportions of the different seed species point to specialization in gathering the most abundant seeds (more so, indeed, than might be expected in view of their density in the environment). Thus, the superabundance of a given seed species in the environment prompts increased activity. This would suggest that *M. barbarus* is a predator specializing in high-density resources, and is able to modulate its efforts as a function of other factors, including resource-mass (which is directly related to energy content).

Reports indicate that various species of this genus are able to respond to a combination of seed abundance and seed size (Detrain & Pasteels 2000, Willot *et al,* 2000). However, the effect of seed size is complex, and may be influenced by other factors, including colony reserve levels (Reyes-López & Fernández-Haeger 2002).

This may have important implications for the structure and composition of grassland. A population of a given herbaceous species, whose seed production is abundant and highly-concentrated in both space and time, may be exposed to high consumption rates in the immediate vicinity of the parent plant (see review in Harper 1977). This effect could be intensified in the case of high-preference seeds.

In contrast, a plant bearing large seeds may reduce predation rates if seed availability coincides with that of other species producing

abundant seeds (i.e. if it accounts for a relatively low proportion of total resource availability), since preference for mass appears to decline in this situation (IM-5 versus IM-30, in the present experiments); this can be seen as a strategy of "escape by hiding" (Risch & Carroll 1986). The great diversity of species found in Mediterranean grassland communities may favor one strategy or another depending on the prevailing circumstances.

A high degree of synchronization in seed production might be expected to improve the chances of survival due to by predator satiation. There is considerable synchronization of seed maturation and production amongst herbaceous species in Mediterranean grassland, governed mainly by the start of the dry season in late spring. But at the same time, harvester ants can store large amounts of seeds in "granaries" within their nests, over substantial periods of time (several months) prior to their consumption. Levels of satiety in these species are thus different from those of other seed-consumers, such as birds or rodents. This is more likely to be a logistical than a physiological response, and is probably related to granary size and general nest activity.

A plant with poorly-synchronized seed production coinciding with the period of harvest-ant activity would thus be at a disadvantage with respect to a better-synchronized species (Harper 1977), unless consumption rates were reduced by spatial distribution.

Seed predation may influence grassland diversity (see Hölldobler & Wilson 1990). Consumption of the most abundant species allows some increase in diversity (Inouye *et al.* 1980, Briese 1981); however, even "rare" or low-production species may be "over-predated", as has been shown for *M. galla* (Gillon *et al.* 1984) in a woodland savanna. This does not necessarily depend on a selective search for these species (although this might occur); our results suggest that it is sufficient for seed-production in "rare" species to coincide in space and time with that of one or more high-preference species, since this would prompt intensive gathering activity in harvester ants. In such circumstances, ants seem to be less selective, and "quantity" prevails over "quality". In other words, more than the effect of general synchronization referred to earlier, the effect would be prompted simply by the simultaneous presence, on a grassland path, of high-preference seeds and "rare" seeds.

It has been argued that production of small seeds may be a strategy for evading ant predation in Mediterranean grassland ("downsizing strategy", Detrain & Pasteels 2000). However, this alone would not appear to represent an effective defence mechanism. Other complemen-

tary mechanisms would be required, such as: (a) low "spot-production" rates, in order to prevent high density being an attraction factor for harvester ants (i.e. overall production is not necessarily low, but is spread out further in time or space); or (b) synchronization of seed production with that of many other species. Additionally, the results obtained here suggest that seed size or mass ceases to be a major factor when relative density is very low (IM-5). Similar findings have been reported for other species, including *Messor* (=*Veromessor*) *pergandei* (Mehlop & Scott 1983).

It should also be considered that *M. barbarus* is able to harvest "whole" fruits, cutting them off the plant itself (Reyes-López & Fernández-Haeger 2001); seeds are then extracted once inside the nest. Individual seed size does not influence this predisposed predation strategy, and limits the value of the defensive mechanism: in such cases, small seed mass no longer affords any real defence.

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