S.J. Willott · S.G. Compton · L.D. Incoll

Foraging, food selection and worker size in the seed harvesting ant *Messor bouvieri*

Abstract Interactions among granivores and seeds depend on the foraging behaviour and morphology of the granivores and on the attributes and availability of seeds. We investigated seed selection by the seed harvesting ant *Messor bouvieri* in three adjacent plant communities in Spain by relating the harvested seeds to those in the seed rain. Preference was positively correlated with seed size and abundance which accounted for 43% and 20% of the variance respectively. Contrary to predictions of central place foraging theory, the size of seeds harvested did not increase with distance from the nest. Inclusion of a less-preferred item in the diet was more strongly related to the abundance of more-preferred items (60% of the variance) than the abundance of the less-preferred item (14% of the variance). Worker size accounted for 20–30% of the variance in the size of harvested seeds, although small workers did not appear to be constrained by load size for the range of seeds available. The body size of ants was significantly larger in the community with the greatest proportion of large seeds, although this was not due to their ability to carry larger loads or due to the greater force required to crush these seeds. The strong preference of *M. bouvieri* for large seeds may have important consequences for the plant communities in which they forage.

Key words Allometry · Granivory · Optimal foraging · Seed predation · Size matching

Introduction

Harvester ants are important post-dispersal seed predators in arid and semi-arid regions of the world, where they can have strong direct and indirect effects on recruitment and population densities of plants (Brown

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et al. 1979a, b; Davidson et al. 1985; Hobbs 1985; Rissing 1986). Ants are selective in the seeds they harvest, often displaying density-dependent foraging (Whitford 1978; Briese and Macauley 1981; Crist and MacMahon 1992; but see Hobbs 1985), and this selectivity may have important consequences for maintaining plant species diversity in these communities (Briese 1982; Kunin 1994). The nature of the seeds harvested by ants will depend both on aspects of the biology and ergonomics of the ants, notably their foraging behaviour and morphology, and the abundance, species composition, size and distribution of seeds in their environment.

A number of models have been developed to predict the foraging behaviour and diet selection of animals, which assume that an optimal solution can be attained to foraging problems (summarised in Stephens and Krebs 1986). One prediction of optimal foraging models is that the inclusion of a less-preferred item in the diet is independent of the abundance of that item, and depends solely on the abundance of preferred food (Schoener 1971; Pyke 1984). In contrast, there are other foraging models which predict density dependence or "prey switching", where inclusion of a food item in the diet is proportional to its abundance (e.g. Rapport 1971; Murdoch et al. 1975; Hughes 1979; Stamps et al. 1981). Optimal foraging models have also been extended to encompass the case where animals return to a central place (e.g. a nest) with the food item (Orians and Pearson 1979). Central place foraging theory predicts that, as energy expended by a forager is proportional to distance travelled, higher ranking prey should be harvested at greater distances from the central place (Orians and Pearson 1979).

However, the results of studies on ants often do not conform to predictions of classical foraging theory (e.g. Holder Bailey and Polis 1987; Morehead and Feener 1998) and foraging models have been modified for the special case of social insects, where a colony may have a large and polymorphic forager population (Oster and Wilson 1978). Ants can maximise their foraging efficiency by size matching, the pairing of sizes of forager and food-item (Oster and Wilson 1978). While this has been

suggested for a number of species, the correlations obtained typically explain little of the variance in food chosen (reviewed in Traniello 1989). Davidson (1978) suggested that seed-harvester ant colonies may be able to adjust the size of new workers to match the sizes of the seeds available to the colony, although this has yet to be demonstrated.

The size, shape, strength and relative abundance of naturally occurring seeds have all been shown to influence selection by harvester ants (Whitford 1978; Briese and Macauley 1981; Davison 1982; Hobbs 1985; Crist and MacMahon 1992; Rodgerson 1998). Similar effects have been demonstrated using seed baits in cafeteria tests (Davidson 1978; Holder Bailey and Polis 1987; Kunin 1994). Despite the merits of using experimentally controlled seed baits, the use of non-native seeds or unrealistic densities of seeds makes the interpretation of these results difficult (Crist and MacMahon 1992). There are further problems with using baits. Foraging ants may specialise on seed types based on previous experience (Fewell and Harrison 1991; Johnson 1991) so their response to a novel set of seeds can change over time. Also, optimal foraging theory assumes that inclusion of a food type in the diet is independent of the abundance of that item, and depends solely on the abundance of more preferred items. While it may be possible to manipulate the density or to rank the preference of seeds presented in a small dish, their acceptability is also likely to depend on the background availability of other seeds within the foraging area.

We measured the species composition, size and abundance of seeds in three adjacent plant communities over two years, and compared these to the seeds harvested by the ant *Messor bouvieri* (Bondroit). Seed rain was used as the measure of resource availability to the ants as granivores largely harvest newly produced seeds, rather than those from the seed bank (Price and Joyner 1997). We then examined which seed attributes accounted for preferences of *M. bouvieri*, and tested the following predictions of foraging theory: (a) size of harvested food items (selectivity) increases with distance from the nest; (b) inclusion of items in the diet depends solely on the abundance of preferred species, rather than density of that item; (c) workers maximise their efficiency by size matching; and (d) the relative size of workers in a community will match that of the available seeds.

Materials and methods

Study site

The Rambla Honda is a dry valley with an ephemeral watercourse in the province of Almería, south-eastern Spain (37°08′N, 2°22′W, 630 m altitude). The climate is semi-arid, with a mean annual rainfall of 256 mm, falling mainly between the months of October and April (Puigdefábregas et al. 1996). The vegetation is typical of the region and may be classified into three relatively distinct communities along a catena from the ridge top to the valley floor, and defined by the dominant perennial in each. On the upper slopes, the plant community is dominated by the tussock-forming perennial

grass *Stipa tenacissima* L. On the alluvial fans formed from material eroded from the upper slopes, the dominant shrub is *Anthyllis cytisoides* L., a drought-deciduous legume growing to a height of 1 m. On the lower slopes and in the valley bottom, another legume, *Retama sphaerocarpa* (L.) Boiss. is dominant, growing up to 3 m tall, with a diverse assemblage of other plants growing under its canopy (Pugnaire et al. 1996). (For clarity, when referring to each of these communities, we use the non-italicised generic names of the dominants, i.e. Retama, Anthyllis and Stipa communities. Conventional italicised names are used when referring to these species in particular.) In each community, most of the other plants are winter annuals, germinating after the autumn rains, flowering in spring, and producing seed in summer.

The seed harvesting ant *M. bouvieri* is found at arid sites throughout the western Mediterranean and North Africa (Bernard 1968). There are ten species of the genus *Messor* in the Iberian Peninsula (Collingwood 1978), but *M. bouvieri* is the only species in the Rambla Honda. Workers reach foraging patches by following conspicuous trunk trails, at the end of which they spread out to search for seeds. Trunk trails may be used for several weeks. Individual workers are single-load foragers (only one food item is collected per trip), and foraging is temperature-dependent (Cerdá et al. 1998). At this site there is little foraging during winter, and timing of activity changes from around midday, to crepuscular and finally to nocturnal as daily temperature increases in summer (S.J. Willott, unpublished data).

Seed attributes

We collected mature seeds from or beneath plants on an ad hoc basis in the summers of 1996, 1997 and 1998. Following removal of all accessory structures we weighed between 30 and 1000 seeds of each species, depending on size, in a single batch, so no estimate of within-species variance is available. We determined seed strength by crushing the seeds between the plates of a force tester (Instron Model 8500, Instron, High Wycombe, UK), with the plates set to move at 3 mm min^{-1}. Seeds from seven species with mean seed mass between 1–7 mg were tested, as these were the preferred food of the ants (see Results).

Seed rain

In the Stipa and Anthyllis communities, we placed 20 seed traps in a 5×4 grid at 5 m spacing. In the Retama community 10 seed traps were located on a stratified random basis in the central 4×10 m area of 10×15 m study plots already established at the site. There are four of these plots, giving a total of 40 traps.

The seed traps followed the design of Rabinowitz and Rapp (1980). Each trap was the lid of a 9-cm petri dish, containing a 9-cm diameter filter paper onto which we applied a permanently sticky gum (Oecomulsion, Oecos, Hitching, UK). The dish was glued to a 9-mm thick piece of plywood through which a 5-cm nail had been driven. The nail was pushed into the soil, so the trap was 1 cm above the soil, preventing the entry of any seeds blown along the surface. We measured seed rain in each community from May to September 1997, and from April to September 1998, replacing the filter papers every 2 weeks initially but at longer intervals later in the summer when seed rain had declined. The traps were in identical positions for both years. We identified and counted seeds on the filter papers, using a dissecting microscope when necessary. The mass per trap was calculated as the product of the number of seeds by the mean mass per seed as determined above. The annual cumulative total of seeds and mass of seed per trap were calculated and, following logarithmic transformation, the effects of community and year were determined by a two-way ANOVA.

Foraging

For each summer month (from June to September, in 1997 and 1998), 20 ants each carrying a food item were collected at random

from returning foraging trails of up to five nests in each plant community. Ants were picked up with forceps and transferred to individual tubes containing 70% (v/v) alcohol. The length of each foraging trail was measured. Ants apparently not carrying anything were periodically collected to ensure that smaller items were not being missed. Seeds were identified in the laboratory and any items that were not seeds were noted.

Food preference

We compared the abundance of seeds collected by ants to their abundance in the seed rain using the α vector preference metric (Chesson 1983), calculated as:

$$\alpha_i = \frac{f_i / r_i}{\sum_{j=1}^{n} f_j / r_j} \tag{1}$$

where f_i = the proportion of seed species i collected by foraging ants; r_i = the proportion of seed species i in the seed rain; f_j = the proportion of seed species j collected by foraging ants; r_j = the proportion of seed species j in the seed rain; n = the number of species. Values of α_i can vary between 0 and 1, and $\Sigma\alpha_i$=1. This normalised estimate of preference is independent of abundance (Chesson 1983). We calculated α for each community and year for those species that comprised more than 5% of the seed rain or of seeds collected by the ants. Following Crist and MacMahon (1992), we used multiple linear regression to examine the effects of seed size and relative abundance on preference. For each community and year we calculated the abundance of food items more preferred than species i by summing the abundance of all species whose values of α were greater than α_i. The effects on food selection of abundance of that food item and abundance of preferred species were also determined by multiple linear regression.

Worker size – load size relationships

Many of the "seeds" carried by the ants are actually fruits because structures associated with the pericarp or the inflorescence may remain attached to the seed after dispersal. These structures are removed in the nest and are discarded to form the characteristic piles of chaff around the entrance. We therefore use the term "load size" rather than "seed size" to avoid confusion. Of the approximately 500 ant-load pairs sampled from each community, 100 ant-load pairs were randomly chosen. These were oven-dried at 70°C to constant mass and the mass of the ant and the load was determined to 0.01 mg. The width of the head and length of the right hind femur of each ant were measured to an accuracy of 0.01 mm.

Results

Seed rain

Seeds of 51 species of plants were recorded, with 33, 29 and 26 species in the Retama, Anthyllis and Stipa communities respectively (Appendix 1). There were significant differences in the number and mass of seeds produced per unit area among communities and years (Fig. 1; Table 1). The Anthyllis community consistently had the greatest mass and number of seeds. The data for the seeds of *Retama sphaerocarpa* are presented separately in Fig. 1a because they are not harvested by *M. bouvieri*. The ants appear unable to grip the smooth, hard testa, so it is inappropriate to include them in an estimate of the resources available to this species. Furthermore, with a mass of approximately 70 mg, seeds of *R.*
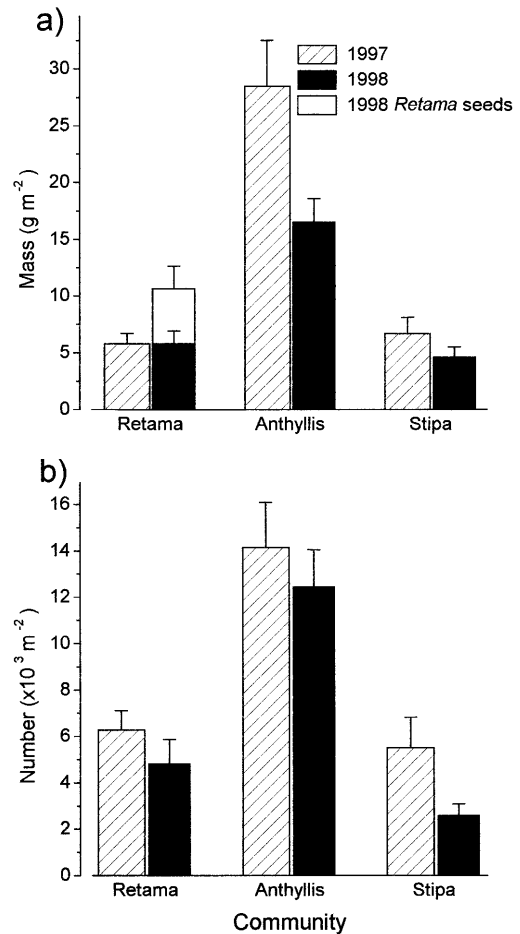

Fig. 1 The cumulative seed rain as measured by **a** mass and **b** number of seeds per unit area in each plant community for 1997 and 1998 (mean +1 SE). For the Retama community, data are presented both with and without the seeds of *R. sphaerocarpa* (see text for details). In Fig. 1b, the difference in number of seeds per unit area due to *R. sphaerocarpa* is too small to be visible at this scale

sphaerocarpa are an order of magnitude larger than the next largest seed and two orders of magnitude greater than the median seed mass (0.75 mg). Only 34 of these seeds were trapped in 1998 (none were produced in 1997 following complete defoliation of all the shrubs in the area by unidentified lepidopteran larvae in 1996). So while having a negligible effect on the number of seeds, they have a strong effect on the total mass of the seed rain.

There was significant variation among communities in the size distribution of seeds (1997: G=17,122, df=6, P<0.0001; 1998: G=4841, df=6, P<0.0001, Fig. 2). Most seeds in the Anthyllis community were >2 mg, while most seeds in the Retama and Stipa communities were <2 mg.

Foraging and food preference

There was no significant difference in the length of foraging trails (log transformed) among communities (F=1.65,

Table 1 The effects of community and year on mass and number of seeds per m² in the seed rain as tested by ANOVA. Data were log transformed prior to analysis. No interaction terms were significant. (The seeds of *Retama sphaerocarpa* were excluded from the analyses – see text for details)

Source of variation	Sum of squares	*df*	*F*	*P*
Mass				
Community	16.188	2	39.980	<0.0001
Year	1.741	1	8.598	0.004
Error	31.178	154		
Number				
Community	10.256	2	36.444	<0.0001
Year	1.452	1	10.318	0.002
Error	21.669	154		

Fig. 3 The relationship between food preference (mean ± SE) and seed mass

The mass and relative abundance of those seeds comprising more than 5% of the seed rain or food items within each community and year are presented in Table 2. For these species, preference, α_i, is strongly dependent on seed masses >1 mg (Fig. 3), and is negligible for seeds whose mass is less than 1 mg. The effects on preference of seed size and relative abundance were determined by multiple regression analysis, giving:

$$\alpha_i = 0.24\,M_i - 0.29\,R_i + 0.21 \tag{2}$$
($r^2 = 0.63$, $n = 38$, $P < 0.0001$)

and where M_i = seed mass of species i (log transformed) and R_i = relative abundance in seed rain of species i (arcsine transformed). Both coefficients were significantly different from zero (M_i: $t = 5.64$, $P < 0.0001$; R_i: $t = -3.39$, $P = 0.002$). There was no significant colinearity between M_i and R_i ($r = -0.27$, $P = 0.103$), allowing us to partition the explained variance of the regression to the two variables through the standard partial regression coefficients (Sokal and Rohlf 1995). Of the variation in preference, 43% was accounted for by seed mass and 20% was accounted for by relative abundance in the seed rain.

The frequency of seeds of species i harvested, F_i, was negatively correlated with the relative abundance of more preferred species ($r = -0.72$, $P < 0.001$), and positively correlated with preference ($r = 0.35$, $P = 0.031$), seed mass ($r = 0.48$, $P = 0.003$) and relative abundance in seed rain ($r = 0.28$, $P = 0.087$). In a multiple regression of these variables against frequency, preference and seed mass were not significant ($P = 0.651$ and $P = 0.840$, respectively) and were removed from the analysis. The subsequent regression equation was:

$$F_i = 0.48\,R_i - 0.51\,R_{\alpha+} + 0.39 \tag{3}$$
($r^2 = 0.74$, $n = 33$, $P < 0.0001$)

where R_i = relative abundance of species i in seed rain (arcsine transformed) and $R_{\alpha+}$ = the relative abundance of more preferred species in the seed rain (arcsine trans-
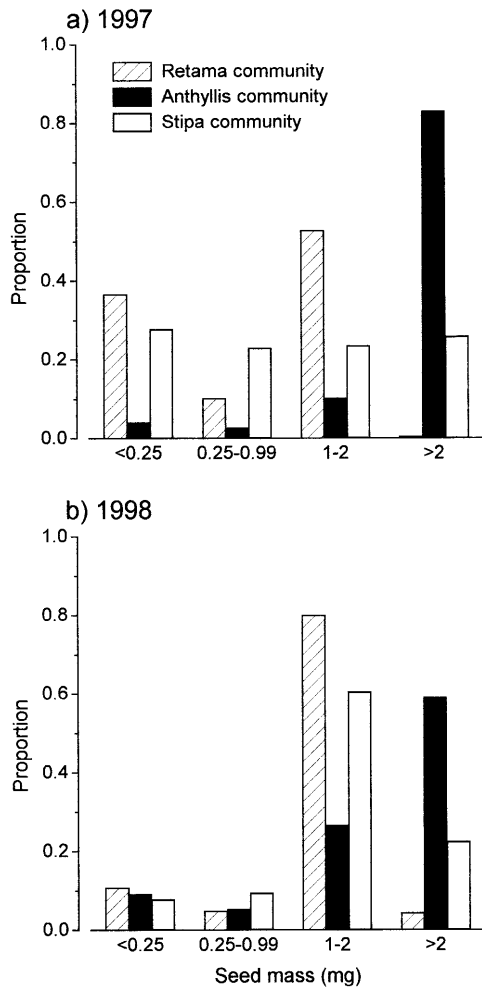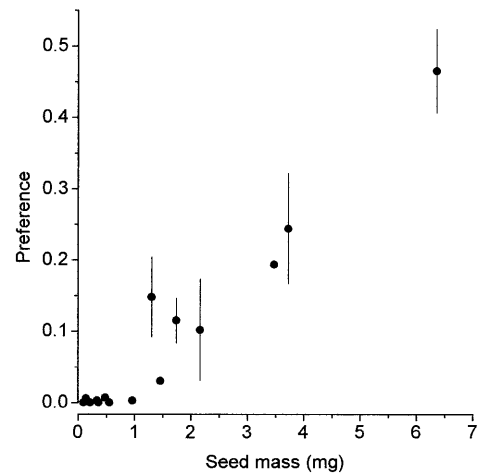

Fig. 2 The distribution by mass of seeds in the three communities in **a** 1997 and **b** 1998

$n = 43$, $P = 0.20$; mean length 10 m, range 3–26 m). Across all communities and years, there was no significant correlation between the length of foraging trail and mean mass ($r = 0.14$, $n = 43$, $P = 0.38$) or minimum mass ($r = 0.01$, $n = 43$, $P = 0.97$) of seeds.
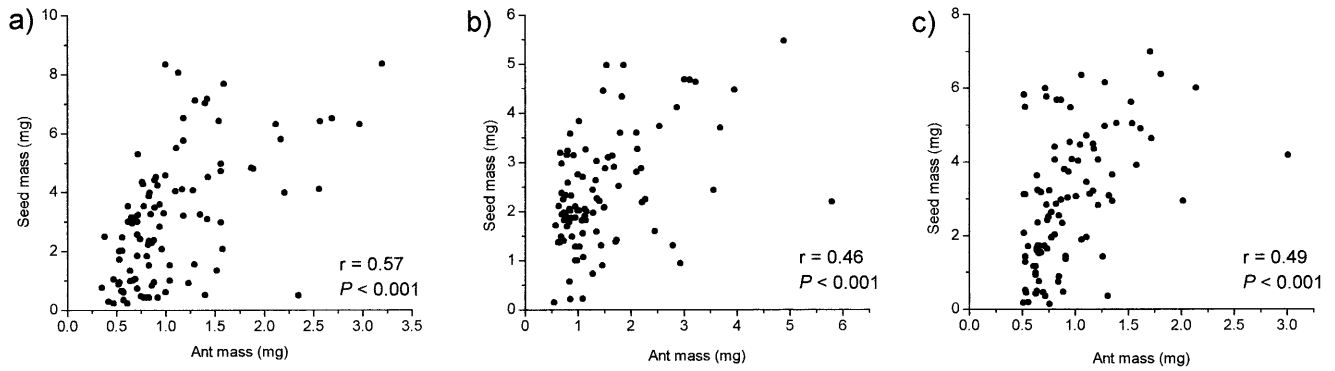
Fig. 4 The relationship between sizes of ants and seeds collected in the **a** Retama, **b** Anthyllis and **c** Stipa communities. Note differences in scales on both axes

Table 2 The mass of seeds (mean/seed) and the proportion (%)of different species in the seed rain (*R*) or returned by foragers (*F*) in the three plant communities of the Rambla Honda in 1997 and 1998. Only those species comprising >5% of either the seed rain or food items within a community and year are included

Species	Mass (mg)	Community					
		Retama		Anthyllis		Stipa	
		R	*F*	*R*	*F*	*R*	*F*
1997							
Stipa capensis	1.31	33.4	34.6	5.0	41.6	17.4	23.8
Stipa tenacissima	3.48	–	–	–	–	5.4	39.6
Brachypodium distachyon	6.36	2.5	20.8	1.2	6.4	0.4	9.6
Avena barbata	3.73	1.9	9.5	1.3	8.2	–	–
Bromus rubens	1.75	4.6	9.1	4.3	5.0	2.7	11.7
Anthyllis cytisoides	2.17	–	–	80.5	27.9	17.7	4.6
Reichardia sp.	0.34	6.9	0.4	–	–	–	–
Tolpis barbata	0.09	23.0	–	–	–	–	–
Asphodelus tenuifolius	1.47	12.2	6.1	–	–	–	–
Minuartia hybrida	0.97	–	–	–	–	13.8	1.7
Plantago albicans	0.49	–	–	–	–	8.1	2.1
Matthiola parviflora	0.22	–	–	–	–	10.6	–
Linum strictum	0.14	–	–	–	–	16.2	0.8
1998							
Stipa capensis	1.31	61.4	43.5	7.1	22.9	38.6	42.2
Brachypodium distachyon	6.36	3.4	24.5	0.6	5.2	7.8	27.6
Avena barbata	3.73	0.8	6.1	–	–	5.9	0.9
Bromus rubens	1.75	3.6	18.4	11.6	21.9	22.7	5.1
Lagurus ovatus	0.56	13.9	–	–	–	–	–
Anthyllis cytisoides	2.17	–	–	38.2	43.2	6.2	13.8
Asterolinon linum-stellatum	0.37	–	–	32.6	–	8.7	–
Silene spp.	0.15	5.4	0.7	–	–	–	–

Table 3 Linear regression analysis of $\log_{10}$ transformed head width (*H*) and $\log_{10}$ transformed hind femur length (*F*) to body mass (*M*) [$\log_{10}$ (mass)$^{1/3}$] of *M. bouvieri* in the three communities. *t*-tests compare regression coefficients with a slope of 1, i.e. isometry. *n.s.* Not significant at *P*=0.05

Community	Best fit equation	r^2	*t*	*P*
Retama	*H*=0.953 *M*–0.013	0.32	–0.336	n.s.
	F=0.615 *M* +0.115	0.21	–3.182	<0.002
Anthyllis	*H*=0.916 *M* +0.059	0.79	–1.714	n.s.
	F=0.747 *M* +0.186	0.67	–4.600	<0.001
Stipa	*H*=0.790 *M*–0.030	0.20	–1.296	n.s.
	F=0.398 *M* +0.101	0.09	–4.493	<0.001

formed). Both coefficients were significantly different from zero (R_i: *t*=5.55, *P*<0.0001; $R_{\alpha+}$: *t* –9.48, *P*<0.0001). There was no significant colinearity between R_i and $R_{\alpha+}$ (*r*=0.25, *P*=0.131). Of the variation in the frequency of seeds harvested, 14% was accounted for by relative abundance in the seed rain and 60% was accounted for by the relative abundance of more preferred species.

Worker size – load size relationships

For the ants in each community, the slopes of the regressions of head width on body mass were not significantly different from 1 (isometry), while the slopes of femur length on body mass were all significantly less than 1, indicating negative allometry (Table 3). This means that

Table 4 The sizes of foraging ants and their loads in each community (mean ± SE; range). Significance tests are from the results of ANOVA on log transformed data. Means with the same letter are not significantly different at the P=0.05 level (post hoc Tukey test following a significant value of F)

Community	n	Ant mass (mg)	Head width (mm)	Femur length (mm)	Load mass (mg)
Retama	99	1.08±0.06[a](0.35–3.20)	0.99±0.03[a](0.48–1.86)	1.32±0.03[a](0.65–1.94)	3.08±0.22 (0.22–8.35)
Anthyllis	94	1.48±0.10[b](0.55–5.79)	1.26±0.03[b](0.93–2.14)	1.65±0.03[b](1.01–2.59)	2.37±0.12(0.14–5.47)
Stipa	95	0.95±0.04[a](0.51–3.01)	0.92±0.02[a](0.40–1.58)	1.26±0.02[a](0.73–1.74)	2.93±0.18(0.14–6.99)
F		16.53	54.09	66.42	1.24
P		<0.0001	<0.0001	<0.0001	n.s.

Table 5 The strength of the seeds (mean ± SE; n =5) of species preferred by ants. Seeds of *Avena barbata*, *Bromus rubens* and *Asphodelus tenuifolius* had no distinct fracture point

Species	Strength (N)
Stipa capensis	24.6± 1.9
Stipa tenacissima	70.0± 4.5
Brachypodium distachyon	123.0±15.7
Anthyllis cytisoides	4.0± 0.2
Avena barbata	–
Bromus rubens	–
Asphodelus tenuifolius	–

heavier ants have proportionately larger heads, but disproportionately shorter legs. For each community, there was a significant correlation between worker size and load size (Fig. 4), with worker size accounting for 21–32% of the variance in the size of collected items.

Ants from the Anthyllis community were significantly larger than those of the Retama and Stipa communities, but there was no significant difference between the communities in the size of their loads (Table 4). The most obvious difference between the preferred seeds in the Anthyllis community and in the other two is the abundance of seeds of *A. cytisoides* itself (see Table 2). If these seeds were significantly stronger than the others (principally grass seeds), then the advantage of larger workers in this community might be their ability to crush these seeds. However, of the seven preferred species which were tested, the seeds of *A. cytisoides* required the least force to crush them (Table 5). Seeds of the most preferred species, *Brachypodium distachyon*, required the greatest force to fracture them, suggesting that within the range of seeds tested here, their strength is not a constraint on selection by *M. bouvieri*.

Discussion

Using the seed rain as the measure of resource availability assumes that ants collect seed from the ground, rather than from plants, and that ants harvest newly-produced seeds (cf. Gordon 1993). In 3 years of observations on *M. bouvieri* at the Rambla Honda, we observed a small number of ants (<10 in a group) climbing annual plants to collect seeds on fewer than 10 occasions (S.J. Willott, personal observation). We conclude that most seeds are collected from the ground. The soil of the Rambla Honda is derived from dark grey micaschist rock (Puigdefábregas et al. 1996) and leaves a fine, dark powder on objects buried in it. Twelve of the approximately 1500 food items collected during the survey were darkened in this way and can be assumed to have been buried in the soil. The remainder were clean, shiny and, we assume, recently produced.

M. bouvieri is highly selective in the seeds it harvests, effectively only harvesting larger seeded species (of mass >1 mg) irrespective of distance from the nest. By using the length of trunk trail as our measure of distance, we will have underestimated the total distance travelled by individual ants (and its variance) as they spread out to search at the end of the trunk trail. However, there was similarly no correlation between total distance travelled and mass of seed harvested for *Pogonomyrmex occidentalis* (Crist and MacMahon 1991) or *Veromessor* (= *Messor*) *pergandei* (Rissing and Pollock 1984), where individual ants were followed, suggesting that this is a common phenomenon in seed harvesting ants.

Several studies have demonstrated that seed selection depended on relative abundance (Whitford 1978; Briese and Macauley 1981; Davison 1982; Hobbs 1985), but although ants harvested seeds of different sizes, size often did not predict the variation in those selected (Whitford 1978; Briese and Macauley 1981; Rissing and Pollock 1984; Hobbs 1985). Relative abundance and size of seeds together accounted for 28% of the variation in food preference of *P. occidentalis* (Crist and MacMahon 1992), but as the two variables were correlated, the relative importance of each could not be separated. For *M. bouvieri* in the Rambla Honda, the two variables were not correlated, and size accounted for 43% and abundance 20% of the variation in preference. The frequency with which seeds of a species were harvested depended principally on the abundance of preferred species (accounting for 60% of the variance), but also on the density of that species (accounting for 14% of the variance).

Optimal foraging models predict that inclusion of an item in the diet should be independent of its density (Stephens and Krebs 1986). The limited density-dependent selectivity in our study may explain why our results do not support a prediction of central place foraging theory. This theory predicts that selectivity increases with distance from the central place as larger loads maximise the rate of energy gain (Orians and Pearson 1979). The se-

lectivity for large seeds shown by M. bouvieri means that seeds of only seven species comprise most of its diet. Of these, *Asphodelus tenuifolius* seeds were only abundant in the Retama community in 1997, and *Stipa tenacissima* seeds in the Stipa community in 1997 (Table 2). Seeds of *S. capensis*, *Bromus rubens* and *A. cytisoides* have similar preference indices (Fig. 3) and also comprise the majority of preferred species in the seed rain of each community (Table 2). The higher ranking species, *Brachypodium distachyon* and *Avena barbata*, are a relatively small component of the seed rain. With these preferred species at low density, and lower-ranking species at high densities, any changes in selectivity with distance will be obscured.

A study of the energetics of foraging in the related *M. capitatus* showed that the costs of foraging were so low that returning almost any seed to the nest would result in a net energetic gain (Baroni-Urbani and Nielsen 1990; Nielsen and Baroni-Urbani 1990). Similar results have been recorded for other seed harvesters (Fewell 1988; Weier and Feener 1995). Applying the parameters for *M. capitatus* to *M. bouvieri*, a 3 mg (dry mass) worker retrieving a 0.2 mg seed from 10 m away at 30°C would expend 0.16 J of energy, while the calorific content of the seed would be 4.28 J (assuming a mean water content of 6.6% and mean calorific content of 22.8 J mg^{-1} dry mass, Baroni-Urbani and Nielsen 1990). So given the potential reward, why does *M. bouvieri* not harvest a greater number of seeds smaller than 1 mg? Combining all communities and years at the Rambla Honda, small-seeded species represent approximately 25% of the number of seeds and 39 of the 51 species recorded, apparently a considerable resource. However, they only comprise 4% of the total biomass of seed. The seven preferred species comprise 77% of the biomass, with the remaining 19% of *Retama sphaerocarpa* seeds which is unavailable to the ants owing to the size and shape of its seeds. So modification of the ants' search behaviour to retrieve small seeds, with the associated time costs, would not necessarily result in the utilisation of a significantly greater proportion of the available biomass of seeds. Ignoring a large proportion of the seeds may be an optimal strategy to minimise time costs, which are thought to be more important than energy costs for some seed harvesting ants (Holder Bailey and Polis 1987; Morehead and Feener 1998). A number of studies of granivore-plant community interactions use total seed number as a measure of abundance (Hobbs 1985; Crist and MacMahon 1992). While this is certainly relevant for plant population processes, it may be a poor estimate of resource availability to highly selective granivores.

Seed-harvester ant colonies may be able to adjust the size of workers produced to match the sizes of the seed resources produced locally (Davidson 1978). While there is variation among communities in the mean size of ants, those in the Anthyllis community being significantly larger (Table 4), this does not appear to be a response to the size of the load carried or strength of the seeds available. Furthermore, although there were significant correlations between ant mass and load mass in each community (also seen in *M. bouvieri* by Retana and Cerdá 1994), there is no strong evidence that smaller ants are constrained in the size of load they may carry, as noted by Crist and MacMahon (1991). The data presented in Fig. 4 suggest that ants less than half the maximum size recorded can carry the largest loads. So why produce larger workers?

Large workers of *M. pergandei* lost water more slowly than small ones and have greater reserves of water, so they can forage for a longer time during the day at temperatures of 40°C or higher (Lighton et al. 1994). We doubt whether this is important for *M. bouvieri* as our observations suggest that they avoid foraging at soil surface temperatures greater than 35°C, switching to nocturnal foraging during summer (S.J. Willott, unpublished data). As time costs are apparently more important than energy costs for seed harvesters (Morehead and Feener 1998), large ants may be favoured as running speed is generally proportional to leg length (Alexander 1982). However, in the genus *Pogonomyrmex*, size had little effect on running speed (Morehead and Feener 1998). Moreover, the negative allometry seen in *M. bouvieri*, where larger ants have disproportionately shorter legs, suggests that this is not the important trait in this species. The advantage of larger ants may be their ability to manipulate or crush seeds of larger diameter, analogous to the value of larger workers of leaf-cutting ants (Wetterer 1994), but we are not aware of any research which shows that post-harvest processing affects seeds selected or morphology of ants. Ant workers may be long-lived, e.g. workers of *M. semirufus* survive for up to 5–6 years (Tohmé and Tohmé 1978), and larger workers of *Eciton burchelli* live longer than smaller ones (Franks 1985). Mass-specific respiratory rates are lower for larger workers (Golly and Gentry 1964; Wilson 1980), as are the mass-specific costs of running (Nielsen and Baroni-Urbani 1990). Thus the benefits to the colony with larger workers may lie in their ability to process larger seeds, and in their relatively lower energy costs and higher longevities rather than in their ability to retrieve certain types of food.

Consequences for the plant community

Species with larger seeds are generally superior competitors (Leishman and Westoby 1994a, b; Marañón and Grubb 1993) but are also selectively preyed upon by *M. bouvieri* in the Rambla Honda. This would suggest that at our site, seed predation by ants has the potential to cause shifts in the plant community from large-seeded to small-seeded species. This contrasts with similar work in North American deserts (e.g. Davidson et al. 1984; Samson et al. 1992) where granivory also affects the composition of the plant community, but where rodents are the dominant consumers of large seeds. In particular, we predict that in the absence of seed predation by ants, the species with the largest (and most preferred) seeds,

Brachypodium distachyon and *Avena barbata*, would be more abundant. We also predict increases in abundance of two further large-seeded grasses, *Aegylops geniculata* (mean seed mass =6.9 mg) and *Hordeum murinum* (mean seed mass =3.8 mg), which were too rare to be included in the present analyses. We have established experimental ant exclosures in the Retama community to test these predictions. With the exception of *Asphodelus tenuifolius* (Liliaceae), all the preferred large-seeded species in the Retama community are grasses, so the winter annual community could become less floristically diverse and dominated by grasses in the absence of ants.

Appendix The total number of seeds in the seed rain of each community of the Rambla Honda in 1997 and 1998. Some of the rarer species could not be identified. Note that there were twice as many traps in the Retama community

Species	Community					
	Retama		Anthyllis		Stipa	
	1997	1998	1997	1998	1997	1998
Poaceae						
Stipa capensis	534	752	91	111	123	126
Stipa tenacissima					38	3
Avena barbata	3	1	24	27	15	19
Brachypodium distachyon	4	42	21	13	3	28
Lamarckia aurea		2				
Schismus barbatus	4	1				
Bromus tectorum		4				
Bromus rubens	74	44	84	182	19	74
Lagurus ovatus	26	17				
Hordeum murinum				9		
Aegylops geniculata	1					
Fabaceae						
Retama sphaerocarpa		34				
Anthyllis cytisoides			1458	615	125	24
Bisserula pelecinus	1					
Medicago minima	4		1			
Ononis viscosa	8	26	37	1		
Hippocrepis multisiliquosa					1	
Asteraceae						
Reichardia sp.	111		1			1
Leontodon sp.	8	1		2	7	
Tolpis barbata	368		1		2	
Centaurea melitensis	2		7	5		
Leysera leyseroides	4					
Hypochoeris glabra	1					
Calendula tripterocarpa			1	1	1	
Calendula arvensis	1	3		1	1	2
Sonchus oleraceus			1			
Andryala ragusina		1				
sp. A	63				1	1
sp. B	1					
Others						
Plantago albicans			2		57	
Linum strictum	53	2	63		114	13
Reseda luteola	1					
Erodium cicutarium	3		4	1		
Eryngium campestre		1			1	

Species	Community					
	Retama		Anthyllis		Stipa	
	1997	1998	1997	1998	1997	1998
Lobularia maritima	14	1	4	17		2
Scabiosa monspeliensis					1	
Asphodelus tenuifolius	195	3	1		21	
Helianthemum salicifolium				3		
Silene spp.	18	66	1			
Matthiola parviflora					75	
Minuartia hybrida			1		97	
Asterolinon linum-stellatum		2	6	56		28
Lavandula multifida						2
sp. C	26	1		22		
sp. D	4			3		
sp. E				1		
sp. F					3	
sp. G				1		
sp. H						2
sp. I						1
sp. J				1		
Number of species	27	20	20	20	20	15

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