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ORIGINAL ARTICLE

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Influence of seed size on feeding preferences and diet composition of three sympatric harvester ants in the central Monte Desert, Argentina

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Abstract Selective seed consumption by harvester ants may affect seed abundance and composition and, ultimately, plant communities. We evaluated the influence of seed size on preferences and diet of *Pogonomyrmex mendozanus*, *P. rastratus*, and *P. inermis* in the central Monte Desert, Argentina. In choice experiments with *Pappophorum* spp. seeds of different sizes, *P. mendozanus* and *P. rastratus* preferred large seeds, maximizing energy reward. *P. inermis* showed a less-marked preference for large seeds, which was probably due to morphological constraints imposed by its small body size. Under natural conditions, none of the three species selected larger *Pappophorum* spp. seeds probably because of high travel and handling costs. Seeds of intermediate size predominated in the diet of the three species but a slight size match was detected as *P. mendozanus* carried larger seeds than *P. rastratus* and this than *P. inermis*, matching body-size differences. Thus, ants probably maximize energy reward but face morphological restrictions and higher costs when carrying and holding large seeds. While seeds of intermediate size are the most vulnerable ones to ant predation, small seeds are favored, as they are abundant in the soil seed bank and lowly predated.

Keywords Ants · Community ecology · Desert ecosystems · *Pogonomyrmex* · Seed size

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Introduction

Harvester ants usually show selective diets and marked preferences for certain seed types in different systems (e.g., Kelrick et al. 1986; Gross et al. 1991; Crist and MacMahon 1992; Andersen et al. 2000; Reyes-López and Fernández-Haeger 2002; Nicolai et al. 2007; Pirk et al. 2009). Selective seed consumption may affect the abundance and spatial distribution of seeds as well as soil seed bank species composition (Whitford 1978; Crist and MacMahon 1992; Mull and MacMahon 1996; Marone et al. 1998), which can ultimately produce changes in plant abundance and composition (Inouye et al. 1980; Samson et al. 1992). The knowledge of factors affecting ants' feeding choices is crucial for predicting the effects of ants on plant communities.

Ants' preferences have been attributed to several seed traits, such as nutritional quality (Kelrick et al. 1986; Crist and MacMahon 1992), concentration of secondary compounds (Carroll and Janzen 1973; Whitford 1978; Buckley 1982), morphology (Pulliam and Brand 1975; Azcárate et al. 2005) and size (Davidson 1977; Kelrick et al. 1986; Crist and MacMahon 1992; Willott et al. 2000). Regarding seed size, optimal foraging theory predicts that animals will feed in a way that maximizes energy intake per unit time (Schoener 1971; Stephens and Krebs 1986), and thus, larger seeds would offer more energetic benefits than smaller ones, as they usually provide a higher energetic content (Kelrick et al. 1986; Crist and MacMahon 1992). Preferences of several ant species have been positively correlated to seed size (Kelrick et al. 1986; Crist and MacMahon 1992). However, as seed size increases, mechanical limitations of fit between seeds and ant mandibles and of lifting and transporting large loads may arise (Davidson 1977; Kaspari 1996). Moreover, handling and transport of bigger loads may demand more time and energy (Holder Bailey and Polis 1987; Morehead and Feener 1998). Workers can maximize the rate of energy return to the colony by matching the size of the seeds collected to their own body size. In various ant communities, a positive relationship between workers' body size and load size has been observed, where smaller species prefer small seeds and larger species prefer large seeds (Davidson 1977) or larger species carry seeds of a broader size range including larger ones (Kaspari 1996). This size match has been argued to promote species coexistence through diet partitioning (Davidson 1977).

Pogonomyrmex mendozanus, *P. rastratus*, and *P. inermis* are three sympatric harvester ant species in the central Monte Desert, Argentina. The taxonomic status of *P. mendozanus* has been recently established (Cuezzo and Claver 2009), and is important to note that in previous publications (Pol and Lopez de Casenave 2004; Pirk et al. 2004, 2007, 2009; Pirk and Lopez de Casenave 2006; Pirk 2007; Pol 2008) we considered the Ñacuñán's population as *P. pronotalis*, following Claver and Fowler (1993). The three species are highly granivorous (Pirk et al. 2004, 2009; Pirk and Lopez de Casenave 2006), preferentially consuming grass to other seed types (Pirk 2007). Their activity is diurnal and spans from spring to autumn (Pol and Lopez de Casenave 2004). *P. mendozanus* and *P. rastratus* colonies have relatively high seed removal rates throughout their activity season (5×10^4 and 6×10^4 seeds/colony, respectively), suggesting potential top-down effects, especially on preferred grasses (Pirk and Lopez de Casenave 2006). Here, we evaluate the influence of seed size on preferences and diets of *P. mendozanus*, *P. rastratus*, and *P. inermis* using different approaches. These ants highly consume polymorphic seeds of the genus *Pappophorum*, providing the opportunity of evaluating the importance of seed size on ants' choices with whole native seeds of different sizes. This can reduce some of the confounding factors that usually operate in multi-seed species studies, where it is difficult to assign mechanisms that may be influencing the preference of granivores for a given seed species. Preferences and selection for *Pappophorum* spp. seeds of different sizes were tested with choice experiments and by comparing their proportion in the diet and in the environment. Size distribution of seeds of different species in the diet was also compared with that in the soil seed bank. Finally, some ant morphological traits associated with seed carriage were measured to try to explain how body size can account for the relationships found and for the differences among species.

Methods

Study area

The study was carried out in the Biosphere Reserve of Ñacuñán (34°03′S–67°54′W), located in the central portion of the Monte Desert, Mendoza Province, Argentina. The main habitat is the open woodland of *Prosopis flexuosa* where individuals of this species and of *Geoffroea decorticans* are scattered within a matrix of perennial tall shrubs (mostly *Larrea divaricata*, but also *Condalia microphylla*, *Capparis atamisquea*, and *Atriplex lampa*), low shrubs (*Lycium* spp., *Junellia aspera* and *Acantholippia seriphioides*), and perennial grasses (e.g., *Trichloris crinita, Pappophorum* spp., *Sporobolus cryptandrus, Aristida* spp.). Annual forb cover (e.g., *Chenopodium papulosum*, *Phacelia artemisioides*) is highly variable from year to year. Ñacuñán's climate is dry, with warm and rainy summers and cold, dry winters. Mean annual temperature is 15.9°C (1972–2004) and mean annual rainfall is 333.5 mm (1972–2004) with high inter annual variation. A total of 75% of the annual rainfall occurs in spring and summer (October–March). Seed production of almost all plants is restricted to summer months.

Pappophorum seeds

Two species of the genus *Pappophorum* (*P. caespitosum* and *P. philippianum*) with visually indistinguishable seeds occur in Ñacuñán. Although seeds collected in the field and harvested by ants are most likely of *P. caespitosum* (the species with the highest cover; Roig 1981), we will refer to them as *Pappophorum* spp. as some *P. philippianum* seeds might as well be included. Seeds employed in choice experiments were collected in the open woodland in December 2004, when seed production was high and seeds were mature. Spikelets of *Pappophorum* spp. were stored in paper bags, placed inside vacuum sealed plastic bags with silica gel, and kept at 4°C until inspection.

Twelve percent of the collected *Pappophorum* spp. spikelets lacked caryopses, whereas 28, 46, and 14% contained one, two, and three caryopses, respectively ($n = 75$). Spikelets with three caryopses consisted of a large, a medium, and a small caryopsis. The smallest and largest caryopses from these spikelets were used in choice experiments. Of these, mature and sound caryopses (i.e., that did not crumble when probed with forceps and lacked signs of fungal attack or other kind of damage) were selected under a stereoscopic microscope. One hundred caryopses of each size class were weighed. Length and width (i.e., length of the major axis and length of the major axis perpendicular to it, respectively) of 20 caryopses of each size class were measured and shape was calculated as the length/width ratio. Large and small caryopses differed in weight, length and width, but not in shape (see Table 1).

Pappophorum choice experiments

Pappophorum caryopses were offered at *Pogonomyrmex mendozanus*, *P. rastratus* and *P. inermis* colonies in February 2005. Five active colonies of each species were randomly selected and ten trials were conducted at each colony. During each trial, a large and a small caryopsis were simultaneously placed on the ground, 1 cm apart (to allow individual workers to inspect both seeds) and

Table 1 Mean (±SE) weight, length, width, and shape (length/width) of large and small *Pappophorum* spp. caryopses employed in choice experiments. Results from one-way ANOVA are shown

	Large	Small	*p* value
Weight (mg)	1.29 ± 0.01	0.42 ± 0.03	< 0.001
Length (mm)	2.37 ± 0.03	1.60 ± 0.03	< 0.001
Width (mm)	1.15 ± 0.02	0.75 ± 0.01	< 0.001
Shape	2.07 ± 0.02	2.14 ± 0.03	0.08

close to the nest entrance, during high foraging activity periods (Pol and Lopez de Casenave 2004). The identity (i.e., large or small) of the first caryopsis, which was removed and taken to the nest by a worker, was recorded in each trial.

The number of times a large caryopsis was removed first was calculated for each colony. Since this variable was homogeneous among the five colonies of each species ($X^2_4 = 1.92$, $p = 0.75$ for *P. mendozanus*; $X^2_4 = 0.32$, $p = 0.99$ for *P. rastratus* and $X^2_4 = 3.68$, $p = 0.45$ for *P. inermis*; Chi-square heterogeneity test; Zar 1996), data were pooled per species to obtain a global result. A Chi-square test was used to determine whether seed size was independent of being removed first. Additionally, a Chi-square homogeneity test was performed to determine if the proportion of large caryopses removed first was homogeneous among ant species. A posteriori partitions of the original contingency table were carried out to determine which species differed from the others in their removal frequency of large caryopses (Siegel and Castellan 1988). Yates correction for continuity was applied when recommended (Zar 1996).

Size selection of *Pappophorum* seeds

In the field, *P. rastratus*' workers generally carry single caryopses of *Pappophorum* spp. (i.e., without bracts like glumes, palea, and lemma) to the nest, while *P. mendozanus* and *P. inermis* carry mostly whole spikelets containing different number of caryopses (Pirk and Lopez de Casenave 2006; Pirk et al. 2007). In order to evaluate if *P. rastratus* selects *Pappophorum* caryopses by their size, caryopses carried to the nest by *P. rastratus*' foragers were manually collected in five colonies of this species in February 2002 and weighed. This collection was performed on a time basis (2 h per colony); thus, a different number of caryopses was obtained per colony ($n = 9$–31), depending on activity levels, which are highly variable among colonies (Pol and Lopez de Casenave 2004). Additionally, 20 caryopses from each of five randomly selected individuals of *Pappophorum* spp. were collected in the study area at the same time and weighed. Mean weight of *Pappophorum* spp. caryopses per colony and per plant ($n = 5$ each) were calculated and compared with a one-way ANOVA.

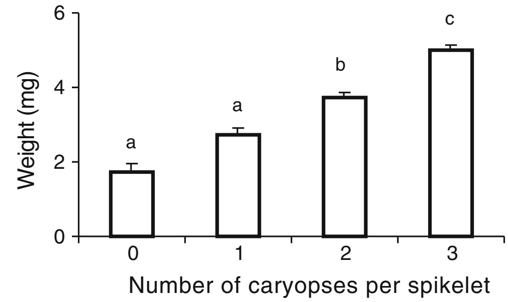

Fig. 1 Mean weight (+SE) of *Pappophorum* spp. spikelets containing 0, 1, 2, and 3 caryopses ($n = 5, 17, 20$, and 15, respectively). *Different letters* indicate significant differences (Scheffé contrasts; $p < 0.05$)

In order to evaluate if *P. inermis*' and *P. mendozanus*' select *Pappophorum* seeds by their size, spikelets were manually collected from incoming foragers in three colonies of each species in February 2004. As weight of spikelets with different number of caryopses differs (Scheffé contrasts, $p < 0.05$, except for spikelets with one or no caryopsis, $p = 0.09$; Fig. 1), number of caryopses per spikelet was used as a surrogate of spikelet weight. A different analysis was performed this time because the variable was not seed weight but number of caryopses per spikelet. The relative frequency of spikelets with a different number of caryopses in the diet was compared to that of spikelets taken from plants ($n = 30$ spikelets) in the study area at the same time with a Chi-square test. Since this variable was homogeneous among the three colonies of each species ($X^2_8 = 12.74$, $p = 0.12$ for *P. mendozanus* and $X^2_8 = 7.88$, $p = 0.44$ for *P. inermis*; Chi-square heterogeneity test; Zar 1996), data were pooled per species to obtain a global result.

Seed size in the diet

Seed size distribution in the diet of the three species was estimated using diet data from Pirk et al. (2009). These data come from a diet sampling that took place at the same study site throughout three consecutive activity seasons (2001–2002, 2002–2003, and 2003–2004). Seeds of different species in the diet were categorized into four size classes (< 0.10, 0.10–039, 0.40–0.69, and ≥0.70 mg) after Marone and Horno (1997) and Peralta and Rossi (1997), and total seeds collected per size class were used in the analyses. Size distribution of seeds in the soil seed bank in the open woodland of Ñacuñán in the summer were taken from a previous work carried out at the same study site (Marone and Horno 1997). Chi-square tests were performed to compare seed-size distribution in the diet of each species and in the soil seed bank. Chi-square tests were also performed to compare size distribution of seeds in the diet among ant species.

Forager morphology

Pogonomymex mendozanus, *P. rastratus*, and *P. inermis* are monomorphic species. Foragers were collected in five colonies of each species in December 2005 and February 2006 and stored in 96% ethanol. Head width (including eyes), mandible length (along its external surface, from the articulatory border to the tip of the masticatory margin), and length of the left hind femur were measured for each individual. These variables were chosen because they are thought to affect foraging performance: head traits are associated with the ability of holding a load, while leg traits are related to the ability of moving a load (Morehead and Feener 1998; Willott et al. 2000). Twenty-five foragers of each species (five per colony) were measured under a stereoscopic microscope (precision: 0.0125 mm). Values of each variable were averaged for each colony. One-way ANOVA analyses and Scheffé contrasts were performed to compare variables across species.

Results

Pappophorum choice experiments

Large caryopses of *Pappophorum* spp. were removed more often than small ones in choice experiments (88% removal of large caryopses for *P. mendozanus* and *P. rastratus* and 66% for *P. inermis*). Frequency of large caryopses removal was significantly higher than that of small caryopses for each species ($X_1^2 = 27.38$, $p < 0.001$ for *P. mendozanus* and *P. rastratus*, and $X_1^2 = 4.5$, $p = 0.03$ for *P. inermis*; Chi-square homogeneity test). Ant species differed in their degree of preference ($X_2^2 = 11.68$, $p < 0.01$; Chi-square homogeneity test). *A posteriori* partitions of the original contingency table showed that removal frequency of large caryopses was homogeneous between *P. mendozanus* and *P. rastratus* (frequencies between species were actually identical after pooling) but not between *P. inermis* and the other species ($X_1^2 = 11.71$, $p < 0.001$), with a lower frequency for *P. inermis*.

Size selection of *Pappophorum* seeds

Weight of *Pappophorum* spp. caryopses carried to the nest by *P. rastratus* did not differ from weight of those on plants (0.61 ± 0.03 and 0.69 ± 0.02 mg, for caryopses carried by foragers and on plants, respectively; one-way ANOVA, $p = 0.29$). Also, the proportion of *Pappophorum* spp. spikelets with different number of caryopses in the diet of *P. mendozanus* and *P. inermis* was similar to that found on plants (Chi-square tests per species were all not significant: $X_4^2 = 4.3$, $p = 0.36$, $n = 92$ in *P. mendozanus*' colonies, and $X_4^2 = 4.1$, $p = 0.39$, $n = 88$ in *P. inermis*' colonies). Thus, ants are not selecting *Pappophorum* spp. caryopses or spikelets by their size, but they are carrying them in relation to their availability.

Seed size in the diet

Ants carried seeds of intermediate size, mostly between 0.10 and 0.39 mg (Fig. 2). The distribution of seed sizes in the diet of each species differed from that in the soil seed bank (Chi-square test, $X_3^2 = 397$ for *P. mendozanus*, $X_3^2 = 395$ for *P. rastratus* and $X_3^2 = 634$ for *P. inermis*, $p < 0.001$ in all cases; Fig. 2). The three species included a lower proportion of seeds <0.10 mg in the diet and *P. mendozanus* and *P. rastratus* a higher proportion of seeds between 0.40 and 0.69 mg than those in the soil seed bank. Size distribution of seeds in the diet also differed among ant species ($X_6^2 = 1035$, $p < 0.01$; Chi-square test). *P. mendozanus* carried larger seeds than *P. rastratus* and this than *P. inermis*. Only *P. mendozanus* and *P. rastratus* carried seeds ≥0.70 mg, being the proportion higher for *P. mendozanus* (Fig. 2).

Forager morphology

The three species differ in their head width, mandible length, and length of the left hind femur (one-way ANOVA for each variable, $p < 0.05$). Except for length of the left hind femur, which did not differ between *P. rastratus* and *P. inermis* (Scheffé contrast, $p = 0.22$), values of other variables differed among species (Scheffé a posteriori contrasts, $p < 0.05$), being *P. inermis* the smallest and *P. mendozanus*, the largest (Table 2).

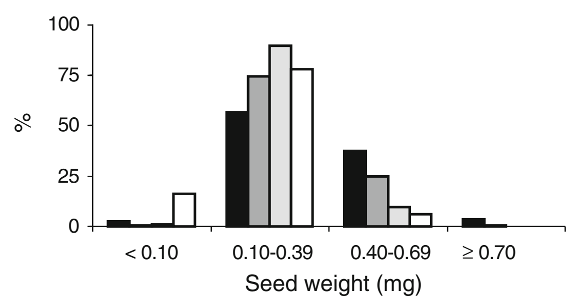

Fig. 2 Percentage of seeds of different size ranges in the diet of *P. mendozanus* (*black bars*, $n = 1341$), *P. rastratus* (*dark grey bars*, $n = 1940$), and *P. inermis* (*light grey bars*, $n = 6518$), and in the soil seed bank (*open bars*, $n = 870$)

Table 2 Mean (±SE) head width (HW), mandible length (ML), and length of the left hind femur (LF) of *Pogonomyrmex* foragers

	HW (mm)	ML (mm)	LF (mm)
P. inermis	1.8 ± 0.03 a	1.05 ± 0.01 a	1.82 ± 0.01 a
P. rastratus	2.03 ± 0.01 b	1.22 ± 0.02 b	1.87 ± 0.02 a
P. mendozanus	2.16 ± 0.02 c	1.32 ± 0.02 c	2.21 ± 0.02 b

Different letters indicate differences between species (Scheffé contrasts; $p < 0.05$)

Discussion

Seed size influences preferences of *Pogonomyrmex mendozanus*, *P. rastratus*, and *P. inermis* in the Monte Desert. Choice experiments close to the nest entrance showed that *Pogonomyrmex mendozanus* and *P. rastratus* prefer large *Pappophorum* spp. caryopses to small ones. Since offered *Pappophorum* caryopses differ only in size, which is usually positively correlated to energy content (Kelrick et al. 1986; Crist and MacMahon 1992), these ants are probably maximizing their energy intake as optimal foraging theory predicts (Schoener 1971; Stephens and Krebs 1986). Similar results were obtained for *P. californicus* using oat fragments of different sizes (Holder Bailey and Polis 1987). For *P. inermis*, however, preferences for large seeds were less marked. This species has the narrowest head and shortest mandibles of the studied species and may face higher morphological restrictions when holding and carrying large loads (Davidson 1977). Field observations during the experiments support this explanation. *P. inermis* had the highest number of unsuccessful attempts of picking up large seeds, twofold higher than that of *P. rastratus* and also than that for small seeds. In contrast, only one unsuccessful attempt of picking each seed type was observed in *P. mendozanus*, the largest species.

Although ants chose large *Pappophorum* spp. caryopses under experimental conditions, they carried caryopses and spikelets similar in size to the ones found in the field. This lack of size selection suggests that under natural conditions other factors could become important and restrict ants' choices. Central place foraging theory predicts that optimal foragers will choose larger items with increasing distance from the central place (Orians and Pearson 1979). However, in some harvester ants this prediction does not hold, because travel and handling times are positively correlated to seed size (Holder Bailey and Polis 1987; Weier and Feener 1995; Morehead and Feener 1998). This is quite relevant for harvester ants, as time costs seem to be more important than energy costs (Fewell 1988; Lighton et al. 1993; Weier and Feener 1995). Carrying larger *Pappophorum* seeds may decrease travel speed and increase handling time in the studied species. Also, since large caryopses and spikelets of *Pappophorum* spp. are infrequent in the environment, selecting them could imply more search time, and thus, a lower overall reward. In contrast, in *Pappophorum* choice experiments large and small caryopses were equally available and placed close to the nest entrance, demanding minimal travel time.

Seeds of intermediate size prevailed in the diet of the studied ants. Thus, they may tend to maximize energy reward but probably face morphological restrictions and higher costs when carrying and holding large seeds. Some differences among species were observed as *P. mendozanus* carried a higher proportion of large seeds than *P. rastratus* and this than *P. inermis*. This pattern could arise from differences in size limit (i.e., the maximum size of seeds an ant can lift and carry; Kaspari 1996) among species, which increases with ant size. Thus, *P. mendozanus*' foragers are capable of carrying larger seeds than *P. rastratus* and this, in turn, larger than *P. inermis*. In choice experiments involving six native species, seeds of intermediate size were also the most preferred ones by these ants (Pirk 2007). No differences were detected among ant species in this case, probably because the largest and low preferred seed (*Larrea divaricata*) was too heavy (7.1 mg) and far beyond size limit of the three species. However, in cases involving several species (i.e., diet and multi-species preference experiments), caution has to be taken when interpreting results only on an energetic basis, since seeds of different species differ in traits other than energy content (e.g., shape, seed nutritional content, presence of secondary compounds), which could also be having an important influence on ants' selection (Carroll and Janzen 1973; Kelrick et al. 1986; Crist and MacMahon 1992; Azcárate et al. 2005).

In spite of the slight size match of *Pogonomyrmex* species in the Monte Desert (i.e., *P. mendozanus* carried larger seeds than *P. rastratus* and this than *P. inermis*, matching body size differences), diet composition is very similar among species, especially between *P. rastratus* and *P. mendozanus* (Pirk and Lopez de Casenave 2006; Pirk et al. 2009). In other studies where a more clear size match was found, body size ranges were wider (e.g., head width 0.5–2.2 mm; Kaspari 1996) than in this study (head width 1.8–2.2 mm). This size difference does not seem large enough to partition diets and promote coexistence. Alternatively, differences in foraging strategy could explain the coexistence of species of similar body size (Davidson 1977). Recently, Pol (2008) found that *P. inermis* has a group foraging strategy while *P. rastratus* and *P. mendozanus* have an individual foraging strategy, but the latter is able to turn into a group forager at high resource levels. Thus, although the three species exploit similar resources, they do it in different ways.

The influence of seed size on diet and preferences of *Pogonomyrmex* species in the central Monte Desert could have consequences on plant community. While seeds of intermediate size are subjected to the highest predation pressure, small and large seeds are less consumed. All species collect a lower proportion of small seeds, and *P. mendozanus* and *P. rastratus* also a higher proportion of large seeds than those available in the soil seed bank (Marone and Horno 1997). Thus, small seeds are probably the most favored ones by ant predation release, as they suffer almost no consumption and are relatively more abundant than large seeds in the soil seed bank (Marone and Horno 1997). In particular, the abundant seeds of the grass *Sporobolus cryptandrus* (~70% of small seeds in the soil seed bank; Marone and Horno 1997) are practically ignored by these ants. Moreover, granivorous birds, which also consume seeds of intermediate size (Marone et al. 1998), show low preference or avoid the seeds of this species (Cueto et al.

2006). The high abundance of *Sporobolus cryptandrus* seeds in the soil seed bank could actually be a consequence of the low predation they suffer. Seed production of this species is high (2×10^7 seeds/ha) but similar to seed production of other grasses, such as *Trichloris crinita* (3×10^7seeds/ha per growing season; Pol et al., unpublished data), which is highly consumed by ants and birds and less abundant in the soil seed bank (< 1% of seeds in the soil seed bank; Marone and Horno 1997). In fact, loss of grass seeds of intermediate size in the soil seed bank in autumn–winter has been attributed to bird consumption (Marone et al. 1998); likewise, ants could be responsible for spring-summer losses.

Finally, seed size is an important factor determining *Pogonomyrmex* ants' preferences and diet in the central Monte Desert. Ants tend to harvest seeds in a way that maximizes their energy reward but are probably subjected to morphological limitations and face higher costs when it comes to carrying large seeds. At the community level, seeds of intermediate size would be more vulnerable to ant predation while small seeds would escape from it. Should seed predation limit seed germination and seedling recruitment in the Monte Desert, plant community could change in time towards small seeded species.

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References

Andersen AN, Azcárate FM, Cowie ID (2000) Seed selection by an exceptionally rich community of harvester ants in the Australian seasonal tropics. J Anim Ecol 69:975–984

Azcárate FM, Arqueros L, Sánchez AM, Peco B (2005) Seed and fruit selection by harvester ants, *Messor barbarus*, in Mediterranean grassland and scrubland. Funct Ecol 19:273–283

Buckley RC (1982) Ant–plant interactions: a world review. In: Buckley RC (ed) Ant–plant interactions in Australia. W Junk, The Hague, pp 111–141

Carroll CR, Janzen DH (1973) Ecology of foraging by ants. Annu Rev Ecol Syst 4:231–257

Claver S, Fowler HG (1993) The ant fauna (Hymenoptera: Formicidae) of the Ñacuñán Biosphere Reserve. Naturalia 18:189–193

Crist TO, MacMahon JA (1992) Harvester ant foraging and shrub-steppe seeds: interactions of seed resources and seed use. Ecology 73:1768–1779

Cueto VR, Marone L, Lopez de Casenave J (2006) Seed preferences in sparrow species of the Monte Desert, Argentina; implications for seed–granivore interactions. Auk 123:358–367

Cuezzo F, Claver S (2009) Two new species of the ant genus *Pogonomyrmex* (Hymenoptera: Formicidae) from Argentina. Rev Soc Entomol Argent 68:97–106

Davidson DW (1977) Species diversity and community organization in desert seed-eating ants. Ecology 58:711–724

Fewell JH (1988) Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. Behav Ecol Sociobiol 22:401–408

Gross CL, Whalen MA, Andrew MH (1991) Seed selection and removal by ants in tropical savanna woodland in Northern Australia. J Trop Ecol 7:99–112

Holder Bailey KH, Polis GA (1987) Optimal and central-place foraging theory applied to a desert harvester ant, *Pogonomyrmex californicus*. Oecologia 72:440–448

Inouye RS, Byers G, Brown JH (1980) Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. Ecology 61:1344–1351

Kaspari M (1996) Worker size and seed size selection by harvester ants in a neotropical forest. Oecologia 105:397–404

Kelrick MI, MacMahon JA, Parmenter RR, Sisson DV (1986) Native seed preferences of shrub-steppe rodents, birds and ants: the relationships of seed attributes and seed use. Oecologia 68:327–337

Lighton JRB, Weier JA, Feener DH Jr (1993) Energetic of locomotion and load carriage in the desert harvester ant *Pogonomyrmex rugosus*. J Exp Biol 181:49–61

Marone L, Horno ME (1997) Seed reserves in the central Monte Desert, Argentina: implications for granivory. J Arid Environ 36:661–670

Marone L, Rossi BE, Lopez de Casenave J (1998) Granivore impact on soil-seed reserves in the Monte Desert, Argentina. Funct Ecol 12:640–645

Morehead SA, Feener DH Jr (1998) Foraging behavior and morphology: seed selection in the harvester ant genus *Pogonomyrmex*. Oecologia 114:548–555

Mull JF, MacMahon JA (1996) Factors determining the spatial variability of seed densities in a shrub-steppe ecosystem: the role of harvester ants. J Arid Environ 32:181–192

Nicolai N, Cook JL, Smeins FE (2007) Grassland composition affects season shifts in seed preference by *Pogonomyrmex barbatus* (Hymenoptera: Myrmicinae) in the Edwards Plateau, Texas. Environ Entomol 36:433–440

Orians GH, Pearson ND (1979) On the theory of central place foraging. In: Horn DJ, Stairs D, Rodger DM (eds) Analysis of ecological systems. Ohio State University Press, Columbus, pp 155–177

Peralta IE, Rossi BE (1997) Guía para el reconocimiento de especies del banco de semillas de la Reserva de la Biósfera de Ñacuñán (Mendoza, Argentina). Boletín de Extensión Científica de IADIZA 3:1–24

Pirk GI (2007) Granivoría por hormigas del género *Pogonomyrmex* en el Monte central: consumo de semillas e impacto sobre el banco de suelo. Doctoral thesis, Universidad de Buenos Aires, Buenos Aires

Pirk GI, Lopez de Casenave J (2006) Diet and seed removal rates by the harvester ants *Pogonomyrmex rastratus* and *Pogonomyrmex pronotalis* in the central Monte Desert, Argentina. Insect Soc 53:119–125

Pirk GI, Lopez de Casenave J, Pol R (2004) Asociación de las hormigas granívoras *Pogonomyrmex pronotalis*, *P. rastratus y P. inermis* con caminos en el Monte central. Ecol Aust 14:65–76

Pirk GI, Lopez de Casenave J, Marone L (2007) Evaluation of different techniques for the study of harvester ants (*Pogonomyrmex* spp.) diet. Environ Entomol 36:1092–1099

Pirk GI, Lopez de Casenave J, Pol R, Marone L, Milesi F (2009) Influence of temporal fluctuations in seed abundance on the diet of harvester ants (*Pogonomyrmex* spp.) in the central Monte Desert, Argentina. Aust Ecol 34:908–919

Pol R (2008) Granivoría por hormigas del género *Pogonomyrmex* en el Monte central: respuestas funcionales a las variaciones en la disponibilidad de semillas. Doctoral thesis, Universidad Nacional de Cuyo, Mendoza

Pol R, Lopez de Casenave J (2004) Activity patterns of harvester ants *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* in the Central Monte Desert, Argentina. J Insect Behav 17:647–661

Pulliam HR, Brand MR (1975) The production and utilization of seeds in plains grassland of southeastern Arizona. Ecology 56:1158–1166

Reyes-López JL, Fernández-Haeger J (2002) Food storage in the nest and seed selectivity in the harvester ant *Messor barbarus* (Hymenoptera: Formicidae). Sociobiology 39:123–128

Roig FA (1981) Flora de la Reserva Ecológica de Ñacuñán. Cuaderno Técnico IADIZA 3–80:5–176

Samson DA, Philippi TE, Davidson DW (1992) Granivory and competition as determinants of annual plant diversity in the Chihuahuan Desert. Oikos 64:61–80

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Syst 2:369–404

Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, Singapore

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton

Weier JA, Feener DH Jr (1995) Foraging in the seed harvester ant genus *Pogonomyrmex*: are energy costs important? Behav Ecol Sociobiol 36:291–300

Whitford WG (1978) Foraging in seed harvester ants *Pogonomyrmex* spp. Ecology 59:185–189

Willott SJ, Compton SG, Incoll LD (2000) Foraging, food selection and worker size in the seed harvesting ant *Messor bouvieri*. Oecologia 125:35–44

Zar JH (1996) Biostatistical analysis, 3rd edn. Prentice Hall, Upper Saddle River, NJ