

Influence of temporal fluctuations in seed abundance on the diet of harvester ants (*Pogonomyrmex* spp.) in the central Monte desert, Argentina

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Abstract Harvester ants usually go through temporal fluctuations in environmental seed abundance and composition which could influence their behaviour and ecology. The aim of this study was to evaluate how these fluctuations influence the diet of *Pogonomyrmex rastratus*, *P. pronotalis* and *P. inermis* (Hymenoptera, Formicidae) in the central Monte desert during three consecutive growing seasons. Although seeds were the main item in the diet, these ants turned more generalist when seed abundance of the most consumed species (grasses *Aristida* spp., *Trichloris crinita*, *Pappophorum* spp., *Digitaria californica* and *Stipa ichu*) was low. Accordingly, diversity of items in the diet decreased with seed abundance in a logarithmical fashion, showing higher foraging efficiency for seeds at higher seed abundance. Seed diversity, however, was not related to seed abundance as ants always included several species in their diet, with alternating prevalence. The proportion of the most consumed species increased logarithmically in the diet of *P. rastratus* and *P. pronotalis* along with their abundance in the environment probably as a consequence of diet switching (from forb and shrub seeds to grass seeds) and by an increase in foraging efficiency at higher seed densities. In contrast, foraging activity of *P. inermis* was very low at low seed abundance and its diet included only the five grasses. Among the most consumed species, proportion in the diet was not associated with relative abundance in the environment. *Aristida* spp., *Pappophorum* spp. and *D. californica* were overall highly selected. However, the flexibility in the diet of *P. pronotalis* and *P. rastratus* and the low foraging activity of *P. inermis* during periods of low resource abundance could attenuate potential top-down effects in the central Monte desert. This study shows that bottom-up effects are important in ant-seed interactions and should be considered when predicting and evaluating ants' effects on seed resources.

Key words: bottom-up effect, desert community, granivory, harvester ant, seed abundance.

INTRODUCTION

In arid environments, rains are discontinuous and unpredictable, producing a large spatial and temporal heterogeneity in primary production (Noy-Meir 1973). This great variability determines the existence of only few reliable food resources on which consumers can specialize (Reichman 1979). Seeds are one of them, as they are abundant in desert soils, they can survive through long droughts, they are rich in energy and nutrients, and they can be collected and stored for later consumption (Brown *et al.* 1979; Kemp 1989).

But although granivory confers on animals some independency from productivity patterns, species-specific plant phenology and rainfall levels often lead to temporal fluctuations in seed abundance and composition (Kemp 1989; Marone *et al.* 1998a) which still affect them. For example, fluctuations in seed resources alter migration patterns of granivores (Pulliam & Parker 1979; Marone 1992; Moncroft *et al.* 2002), modify their abundance (Grant 1986; Schluter & Repasky 1991; Schnurr *et al.* 2002) and change their behaviour and ecology (Mehlhop & Scott 1983; Crist & MacMahon 1992; Wilby & Shachak 2000; Hulme & Benkman 2002), at several temporal and spatial scales. Conversely, selective seed consumption by granivores may affect the abundance, composition and

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distribution of seeds (Whitford 1978; Brown *et al.* 1979; Crist & MacMahon 1992; Mull & MacMahon 1996; Marone *et al.* 1998b) which can ultimately produce changes in plant composition and abundance (Brown *et al.* 1979; Inouye *et al.* 1980; Samson *et al.* 1992; Heske *et al.* 1993; Guo *et al.* 1995). As seeds and granivores are reciprocally affected, it is important to study how seed abundance, distribution and composition affect the abundance, ecology and behaviour of their consumers (i.e. bottom-up effects) in order to predict more accurately the effects of granivores on seed resources (i.e. top-down effects), and therefore, to thoroughly understand seed-granivore interactions.

Harvester ants are highly specialized in seed collecting, but occasionally also collect a variety of non-seed items, such as flowers, plant parts, insects and vertebrate faeces (Whitford 1978; Mehlhop & Scott 1983; Hölldobler & Wilson 1990; MacMahon *et al.* 2000; Pirk & Lopez de Casenave 2006). Several studies have shown important temporal variations in harvester ant diet associated with fluctuations in seed abundance (Whitford 1978; Mehlhop & Scott 1983; Rissing 1988). In the Chihuahuan desert, *Pogonomyrmex desertorum* takes seeds in relation to their availability but concentrates on grass seeds late in the growing season, when they become more abundant (Whitford 1978). Studies on harvester ants of the genus *Messor* also showed that ants switch their diet towards less preferred seeds when the most preferred ones are scarce (Tevis 1958; Hölldobler & Wilson 1990; Wilby & Shachak 2000), the basic qualitative prediction of the classic 'diet' model of foraging theory (MacArthur & Pianka 1966; Schoener 1971; Pulliam 1985; Stephens & Krebs 1986). This illustrates how changes in seed abundance can promote functional responses in harvester ant populations: diet breadth should increase in lean periods through the incorporation of various less-preferred items.

Pogonomyrmex rastratus Mayr, *P. pronotalis* Santschi and *P. inermis* Forel (Hymenoptera: Formicidae) are three sympatric harvester ant species in the central Monte desert, Argentina (Claver & Fowler 1993; Pirk *et al.* 2004). Their diet is highly granivorous, with a prevalence of grass seeds (Pirk *et al.* 2004; Pirk & Lopez de Casenave 2006). They have diurnal activity which spans from spring to autumn (Pol & Lopez de Casenave 2004). *Pogonomyrmex rastratus* and *P. pronotalis* colonies have relatively high seed removal rates throughout their activity season (6×10^4 and 5×10^4 seeds colony⁻¹, respectively), suggesting potential top-down effects, especially on preferred grasses (Pirk & Lopez de Casenave 2006). During their activity season, seeds of different species are produced at different times: grasses set seed by the end of the summer (Marone & Horno 1997), even during dry years (R. Pol, G. Pirk & L. Marone, unpubl. data); most forbs germinate in spring with the first rains of

the wet season, with their seed production decreasing strongly during dry periods; and shrubs generally produce seeds before grasses and are even less sensitive to rainfall levels (Marone *et al.* 1998a). As *Pogonomyrmex* species in the central Monte desert appear to concentrate their foraging on newly produced seeds (Pirk 2007), like other harvester ant species (Price & Joyner 1997), these temporal variations in resource abundance should influence their diet composition, and consequently, their potential effects on plants. This study focused on bottom-up effects, evaluating how the fluctuations in seed abundance and composition over three consecutive growing seasons influence the diet of the three harvester ants of the central Monte desert. We studied the association between diet diversity and abundance of the most consumed seeds in the environment, expecting a more diverse diet at low abundance. We also analysed the relationship between the proportion in the diet and abundance in the environment of the most consumed seeds, expecting it to be positive. Finally, we studied whether the proportion in the environment influences the proportion in the diet of each of the most consumed species, and whether ants select them.

METHODS

Study area

The study was carried out in the Biosphere Reserve of Ñacuñán (34°03'S, 67°54'W), in the central portion of the Monte desert, Mendoza Province, Argentina. The main habitat of the reserve is the algarrobal, an open woodland where *Prosopis flexuosa*, and *Geoffroea decorticans* trees are scattered within a matrix of perennial tall shrubs (mostly *Larrea divaricata*, but also *Condalia microphylla*, *Capparis atamisquea*, *Atriplex lampa* and *L. cuneifolia*), low shrubs (*Lycium* spp., *Junellia aspera* and *Acantholippia seriphoides*), and perennial C₃ (*Stipa ichu*) and C₄ (e.g. *Trichloris crinita*, *Pappophorum* spp., *Sporobolus cryptandrus*, *Aristida* spp., *Digitaria californica*, *Setaria leucopila*) grasses. Forb cover (e.g. *Chenopodium papulosum*, *Phacelia artemisioides*, *Parthenium hysterophorus*) is highly variable from year to year. Ñacuñán's climate is dry and highly seasonal. Mean annual temperature is 15.9°C (1972–2004) and mean annual rainfall is 342 mm with high inter annual variation (range: 91–585 mm; 1972–2004). A total of 75% of the rainfall occurs in spring and summer (October–March).

Seed abundance

Seed abundance of the grasses *Aristida* spp., *T. crinita*, *Pappophorum* spp., *D. californica* and *S. ichu*, the species

most consumed by *P. rastratus*, *P. pronotalis* and *P. inermis* (Pirk *et al.* 2004; Pirk & Lopez de Casenave 2006) was estimated on four occasions (October, December, February and April) over each of three growing seasons (2001–2002, 2002–2003 and 2003–2004). These ants mainly forage recently produced seeds from the soil, in overall good conditions (i.e. with no signs of fungal attack or any external damage; Pirk 2007; Pol 2008). We estimated the standing crop of these species, which generally disperse their seeds shortly after they mature (Marone *et al.* 1998a), assuming it as a surrogate of the temporal variation in seed abundance available to these ants (as assumed in previous studies, e.g. Whitford 1978). Abundance of recently produced, undamaged seeds of each species per hectare was calculated as the average number of seeds per individual on every sampling occasion multiplied by the average number of individual plants per hectare, which we assumed constant during the study period. Plant density of each species was estimated in December 2003 by counting the number of reproductive plants in 400 quadrats of 1 × 1 m deployed every 10 m on a 40 × 10 grid (= 4 ha) in the open woodland. The average number of seeds per individual was estimated by removing all the spikes from 10 reproductive individuals of each species randomly chosen on every occasion from the same area. Seeds were removed from the spikes in the laboratory, checked under a stereoscopic microscope for good condition (i.e. undamaged mature seeds that did not crumble when probed with forceps; Mull and MacMahon (1996)) and counted. Seed abundance of the five species was added to obtain the total seed abundance of the most consumed species.

Diet

The diet of the three species was evaluated using three techniques: (i) hand collection of items brought back to the nest by foragers; (ii) collection of items with a semiautomated device with pitfall traps; and (iii) collection of middens. The hand collection technique consisted in picking up at least 20 returning foragers with their loads at each nest entrance with the help of forceps and a teaspoon. The semi-automated collecting device was a circular plastic enclosure placed around the nest entrance, with four pairs of openings (an ‘entrance’ and an ‘exit’ per pair) with soil ramps allowing ant access on the corresponding side of the enclosure. Pitfall traps were set into the ground inside the enclosure, below the entrances, so that incoming ants were captured and their forage could be collected. For the midden collection, a teaspoon-full sample (approximately 3 cm³) was taken of dense areas of *P. inermis*’ middens (the only species which present conspicuous external middens). For a more detailed

description of these techniques, see Pirk *et al.* (2007). As the three techniques were overall effective and consistent in the estimation of the diet of these species (Pirk *et al.* 2007), we used 1–3 techniques per nest on each sampling occasion, depending on particular field conditions (e.g. middens can only be collected by the end of the summer, when they become accumulated).

Samples were taken during activity seasons 2001–2002, 2002–2003 and 2003–2004, on the same four occasions (except for October 2002, when no sampling was performed) and in the same area as seed abundance estimation (see above). On every occasion, 1–6 colonies of each species were sampled (depending on the abundance of colonies with foraging activity). Only estimations based on at least 10 items were considered to represent the diet of a colony on any sampling occasion. The absence or extremely low levels of foraging activity of *P. inermis* in December 2002 and of *P. rastratus* and *P. inermis* in October 2003 prevented the collection of the minimum number of items

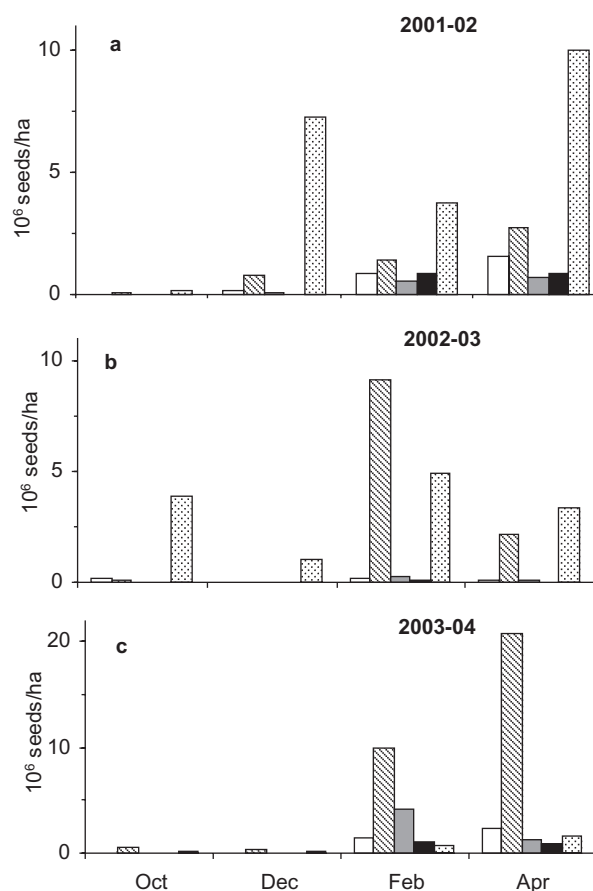


Fig. 1. Seed abundance of *Aristida* spp. (white), *Trichloris crinita* (oblique lines), *Pappophorum* spp. (dark grey), *Digitaria californica* (black) and *Stipa ichu* (spotted) in the central Monte desert in October, December, February and April (a) 2001–2002, (b) 2002–2003 and (c) 2003–2004.

required. Thus, the diet of *P. pronotalis*, *P. rastratus* and *P. inermis* was estimated on 11, 10 and 9 occasions, respectively.

Items collected with the three techniques were identified and counted in the laboratory. Each item was assigned to one of the following categories: (i) seeds; (ii) flowers; (iii) fruits (excluding grass caryopses, considered as seeds; see Whitford (1978)); (iv) vegetative plant parts (non-reproductive structures of plants such as leaves or stem pieces); (v) invertebrates (either partial or complete); and (vi) other items (e.g. vertebrate feces, soil fragments). Seeds were identified to at least genus level. The percentage of each type of item (over total number of items) and species of seed (over total number of seeds) per colony was averaged across colonies of each ant species per sampling occasion. When more than one technique was employed, data were pooled.

Diversity of items and of seed species in the diet were calculated with the Shannon–Wiener index. As total number of items and of seeds obtained differed among colonies, index values were standardized to be based on the same number of items or seeds (i.e. rarefied to the minimum number of 10 items or 10 seeds), using EcoSim Version 7.0 (Gotelli & Entsminger 2001). Kruskal–Wallis tests were used to compare diversity of items and of seeds between species, using colonies as replicates. Dunn’s contrasts were performed after significant differences were obtained (Zar 1996).

Total seed abundance-diet association

The association between seed abundance of the five most consumed species and (i) diversity of items; (ii)

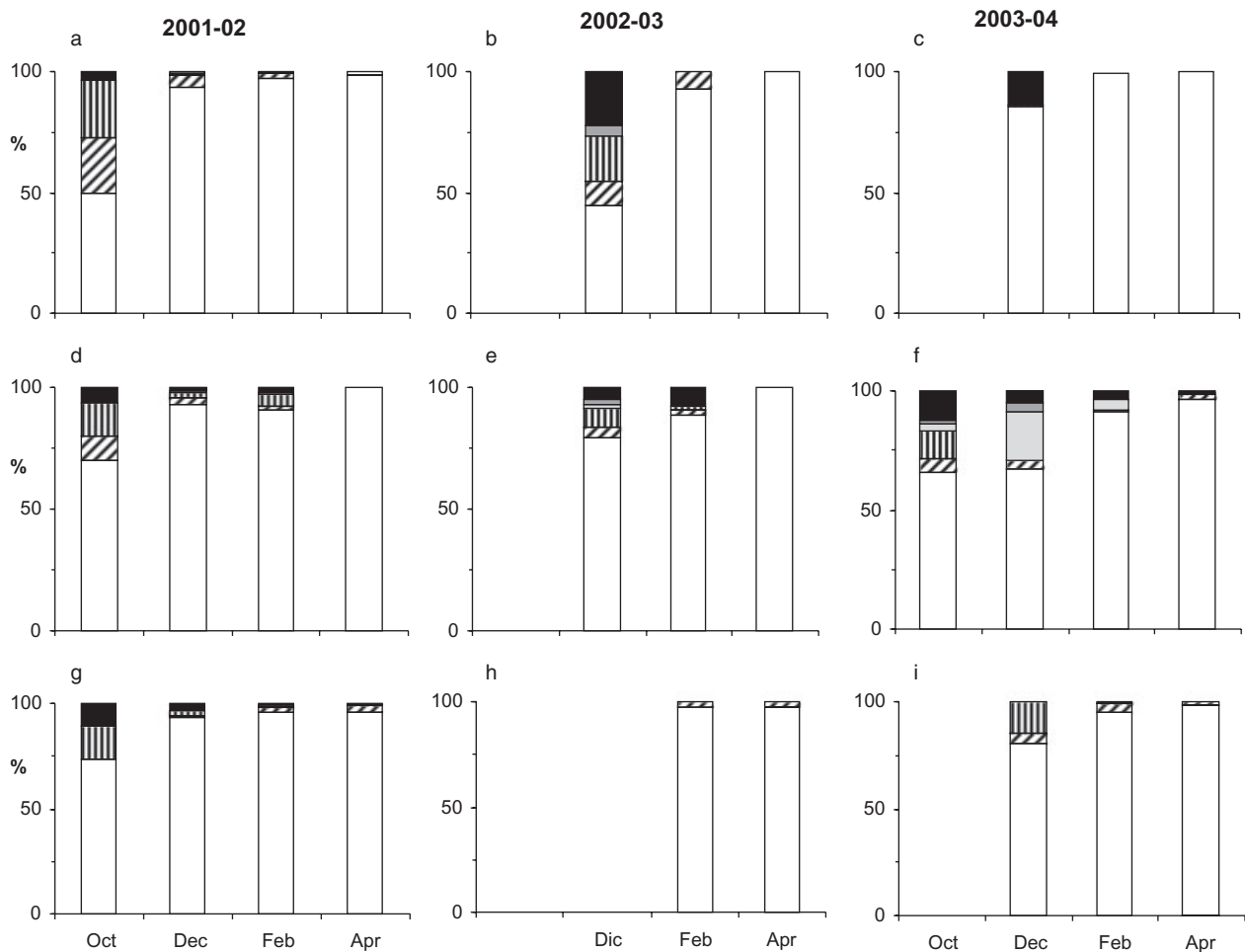


Fig. 2. Mean percentage of seeds (white), vegetative plant structures (oblique lines), invertebrates (vertical lines), fruits (light grey), flowers (dark grey) and other items (black) in the diet of (a–c) *Pogonomyrmex rastratus*, (d–f) *P. pronotalis* and (g–i) *P. inermis* in October, December, February and April (a,d,g) 2001–2002, (b,e,h) 2002–2003 and (c,f,i) 2003–2004 in the central Monte desert. Number of colonies sampled is indicated in Tables 1–3.

diversity of seed species; and (iii) percentage of seeds of the most consumed species in the diet were analysed with linear regressions. Residuals of these analyses were plotted against fitted values to check if they fitted well into a linear model (Gotelli & Ellison 2004). In most cases in which the regression was significant, a better fit was achieved by log-transforming seed abundance.

Relative seed abundance-diet association

The association between percentage in the diet and in the environment of each of the most consumed species (over total number of seeds of the five most consumed species) was analysed using the 95% confidence interval for the concordance correlation coefficient (Zar 1996). Intervals approaching one indicate that seeds are taken in proportion to their availability, whereas intervals which lie far from one indicate selection, either positive (i.e. proportion of seeds in the diet is

higher than in the environment) or negative (i.e. proportion of seeds in the diet is lower than in the environment).

RESULTS

Seed abundance of *Aristida* spp., *T. crinita*, *Pappophorum* spp., *D. californica* and *S. ichu* varied greatly all through each growing season (Fig. 1). It was generally lower in October and December than in February and April, for all species except *S. ichu*, whose production started earlier in the first two studied years (in

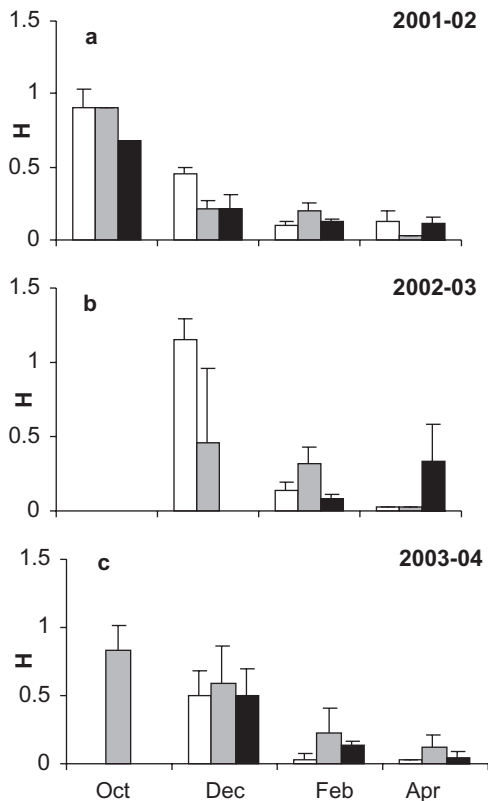


Fig. 3. Mean (+standard error) diversity (*H*: Shannon–Wiener diversity index) of items (seeds, vegetative plant structures, fruits, flowers and other items) in the diet of *P. rastratus* (white), *P. pronotalis* (grey) and *P. inermis* (black) in October, December, February and April (a) 2001–2002, (b) 2002–2003 and (c) 2003–2004 in the central Monte desert. Number of colonies sampled is indicated in Tables 1–3.

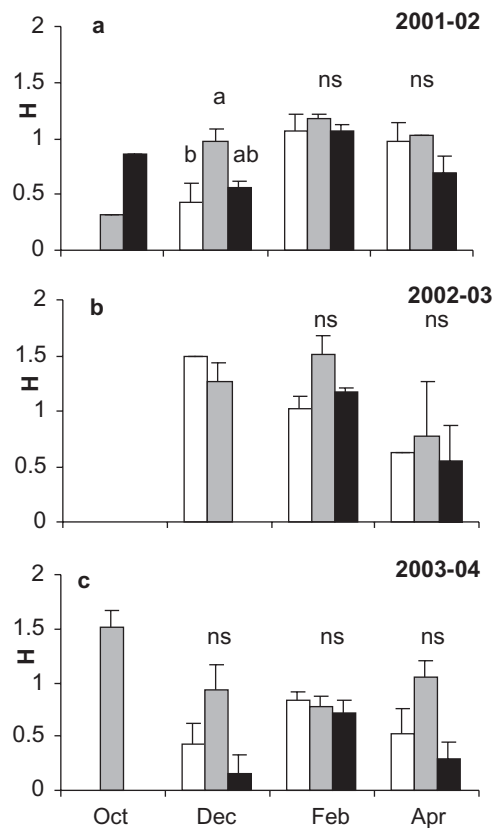


Fig. 4. Mean (+standard error) diversity of seeds species (*H*: Shannon–Wiener diversity index) in the diet of *P. rastratus* (white), *P. pronotalis* (grey) and *P. inermis* (black) in October, December, February and April (a) 2001–2002, (b) 2002–2003 and (c) 2003–2004 in the central Monte desert. ‘ns’ indicates non-significant differences among ant species (Kruskal–Wallis test; $P > 0.05$), different letters stand for significant differences between species (Dunn’s contrasts; $P < 0.05$) and absence of letters indicate occasions on which no statistical tests were performed due to the low number of colonies. Number of colonies as in Tables 1–3, minus those in which fewer than 10 seeds were collected (3 and 2 colonies of *P. rastratus* in October 2001 and December 2002, respectively; 1 colony of *P. pronotalis* in February 2002, October 2003 and December 2003; and 1 colony of *P. inermis* in December 2003).

Table 1. Mean percentage of seeds of different species in the diet of *Pogonomyrmex rastratus* in October (O), December (D), February (F) and April (A) 2001–2002, 2002–2003 and 2003–2004 in the central Monte desert

| <i>Pogonomyrmex rastratus</i> | 2001–2002 | | | | 2002–2003 | | | 2003–2004 | | |
|----------------------------------|------------|--------------|--------------|------------|--------------|--------------|--------------|--------------|------------|------------|
| | O | D | F | A | D | F | A | D | F | A |
| Grasses | 100 | 96.45 | 89.87 | 100 | 40.60 | 94.74 | 90.00 | 22.34 | 100 | 100 |
| <i>Aristida</i> spp. | 43.06 | 4.13 | 45.58 | 24.5 | 16.67 | 23.03 | 5.00 | 1.67 | 17.75 | 4.76 |
| <i>Trichloris crinita</i> | 12.50 | 7.22 | 15.34 | 52.4 | – | 49.08 | 80.00 | – | 3.11 | 10.71 |
| <i>Pappophorum</i> spp. | 11.11 | 1.50 | 13.40 | 6.4 | 10.68 | – | – | 20.67 | 37.24 | 77.38 |
| <i>Digitaria californica</i> | – | 0.05 | 4.63 | 4.2 | – | 2.50 | – | – | 40.00 | 5.95 |
| <i>Stipa ichu</i> | 11.11 | 83.36 | 9.05 | 6.3 | 13.25 | 20.13 | 5.00 | – | – | – |
| <i>Setaria leucopila</i> | – | 0.05 | 0.34 | – | – | – | – | – | 1.90 | 1.19 |
| <i>Sporobolus cryptandrus</i> | 22.22 | – | – | – | – | – | – | – | – | – |
| <i>Chloris castilloana</i> | – | 0.05 | 1.52 | 4.2 | – | – | – | – | – | – |
| <i>Diplachne dubia</i> | – | – | – | 2.1 | – | – | – | – | – | – |
| <i>Neobouteloua lophostachya</i> | – | 0.05 | – | – | – | – | – | – | – | – |
| Forbs | – | 3.37 | 9.95 | – | 46.15 | 5.26 | 5.00 | – | – | – |
| <i>Chenopodium papulosum</i> | – | – | 0.18 | – | – | – | – | – | – | – |
| <i>Conyza</i> spp. | – | 0.29 | 0.71 | – | – | – | – | – | – | – |
| <i>Lactuca serriola</i> | – | 0.05 | 0.65 | – | – | – | – | – | – | – |
| <i>Parthenium hysterophorus</i> | – | 3.03 | 8.41 | – | 46.15 | 5.26 | 5.00 | – | – | – |
| Shrubs | – | 0.08 | – | – | 13.25 | – | 5.00 | 77.66 | – | – |
| <i>Atriplex lampa</i> | – | – | – | – | 2.56 | – | – | 77.66 | – | – |
| <i>Junellia aspera</i> | – | – | – | – | 8.12 | – | 5.00 | – | – | – |
| <i>Larrea</i> spp. | – | 0.08 | – | – | 2.56 | – | – | – | – | – |
| Unidentified | – | 0.11 | 0.18 | – | – | – | – | – | – | – |
| Number of colonies | 3 | 5 | 5 | 4 | 3 | 2 | 1 | 3 | 3 | 3 |
| Total number of seeds | 17 | 804 | 550 | 158 | 25 | 39 | 20 | 64 | 97 | 84 |

Bold numbers are total percentages of each seed type.

December 2001 and in October 2002, respectively). Seeds of *T. crinita* and *S. ichu* were the most abundant (Fig. 1).

Most items carried by *P. rastratus*, *P. pronotalis* and *P. inermis* were seeds (Fig. 2). Although seeds always prevailed over other types of items, their percentage showed parallel temporal variations in the three ant species. The lowest percentages appeared in October and December, whereas in February and April the diet was almost completely made up of seeds. Vegetative plant parts, invertebrates and other items (e.g. vertebrate feces, soil fragments) increased in importance in October and December, though they never exceeded 30% of collected items. Fruits and flowers were, in general, poorly represented. Diversity of items in the diet decreased gradually throughout each season and did not differ among species on any occasion (Kruskal–Wallis test, $P > 0.05$, Fig. 3).

Among seeds, *T. crinita*, *Pappophorum* spp., *Aristida* spp. and *S. ichu* were prevalent in the diet of *P. rastratus* (Table 1), *Aristida* spp., *Pappophorum* spp. and *T. crinita* in the diet of *P. pronotalis* (Table 2) and *Pappophorum* spp., *D. californica*, *T. crinita* and *S. ichu* in the diet of *P. inermis* diet (Table 3). Other seeds with low average values were occasionally abundant in the diet (*S. cryptandrus*, *D. californica*, *A. lampa* and *P. hysterophorus* were important for *P. rastratus*; *S. cryptandrus*,

S. ichu, *D. californica*, *Cryptandra mendocina*, *A. lampa* and *Larrea* spp. for *P. pronotalis*; only *Aristida* spp. for *P. inermis*; Tables 1–3). While *P. rastratus* and *P. pronotalis* eventually foraged relatively high proportions of forb and shrub seeds (e.g. December 2002 and December 2003), *P. inermis* kept an almost exclusively grass seeds diet on every occasion.

As regards temporal variations, forb and shrub seeds presented higher percentages in the diet of *P. rastratus* and *P. pronotalis* at the beginning of each season (Tables 1 and 2). Percentages of the most consumed species varied among sampling occasions, but no clear pattern was detected except for *S. ichu*, which was highly represented in the diet of the three species at the beginning of each season (but not later), and *T. crinita* and *D. californica*, which tended to increase towards the end of each season in the diet of *P. rastratus* and *P. inermis*, respectively (Tables 1–3).

Diversity of seeds in the diet showed variations among sampling occasions but no consistent pattern was observed among seasons (Fig. 4). Although the diet of *P. pronotalis* tended to be the most diverse, it was only statistically different from any of those of the other two species in December 2001, when it differed significantly from the diet of *P. rastratus* (Kruskal–Wallis test, $P < 0.05$; Dunn's contrasts, $P < 0.05$; Fig. 4). On that occasion, *P. rastratus*

Table 2. Mean percentage of seeds of different species in the diet of *Pogonomyrmex pronotalis* in October (O), December (D), February (F) and April (A) 2001–2002, 2002–2003 and 2003–2004 in the central Monte desert

| <i>Pogonomyrmex pronotalis</i> | 2001–2002 | | | | 2002–2003 | | | 2003–2004 | | | |
|----------------------------------|--------------|--------------|--------------|------------|--------------|--------------|--------------|--------------|--------------|--------------|------------|
| | O | D | F | A | D | F | A | O | D | F | A |
| Grasses | 90.48 | 92.75 | 92.67 | 100 | 20.13 | 80.03 | 98.00 | 85.22 | 12.79 | 96.57 | 100 |
| <i>Aristida</i> spp. | 85.71 | 27.72 | 50.01 | 42.11 | 1.39 | 25.90 | 12.00 | 11.67 | – | 7.40 | 32.13 |
| <i>Trichloris crinita</i> | – | 9.03 | 19.12 | 34.21 | – | 9.23 | 25.00 | 11.90 | – | 9.17 | 20.63 |
| <i>Pappophorum</i> spp. | – | 10.25 | 8.78 | 2.63 | 9.93 | 26.84 | 57.00 | 19.82 | 9.43 | 70.84 | 20.36 |
| <i>Digitaria californica</i> | – | 1.04 | 10.22 | 21.05 | – | 5.90 | – | – | 1.52 | 8.08 | 20.63 |
| <i>Stipa ichu</i> | 4.76 | 41.60 | 0.63 | – | 3.82 | 6.08 | 2.00 | 4.17 | – | – | – |
| <i>Setaria leucopila</i> | – | 0.94 | 1.50 | – | 2.50 | 6.08 | 2.00 | 3.59 | – | 1.08 | 1.79 |
| <i>Sporobolus cryptandrus</i> | – | – | – | – | – | – | – | 26.66 | – | – | 4.46 |
| <i>Chloris castilloana</i> | – | – | 1.98 | – | 2.50 | – | – | 7.42 | 1.85 | – | – |
| <i>Schismus barbatus</i> | – | 1.53 | – | – | – | – | – | – | – | – | – |
| <i>Neobouteloua lophostachya</i> | – | – | 0.44 | – | – | – | – | – | – | – | – |
| <i>Bromus</i> sp. | – | 0.64 | – | – | – | – | – | – | – | – | – |
| Forbs | 4.76 | 3.01 | 6.54 | – | 36.59 | 13.12 | – | 5.51 | 1.85 | 1.08 | – |
| <i>Chenopodium papulosum</i> | – | 0.19 | – | – | – | – | – | 1.67 | – | – | – |
| Asteraceae 1 | – | – | – | – | – | – | – | 1.92 | – | – | – |
| <i>Conyza</i> spp. | – | 0.27 | 0.96 | – | – | – | – | – | – | – | – |
| <i>Cryptandra mendocina</i> | – | – | – | – | 20.20 | – | – | – | – | – | – |
| <i>Glandularia mendocina</i> | – | – | – | – | – | 11.45 | – | – | – | – | – |
| <i>Lactuca serriola</i> | – | – | 0.25 | – | – | – | – | – | – | – | – |
| <i>Lappula redowski</i> | 4.76 | 0.19 | 0.22 | – | – | – | – | – | – | – | – |
| <i>Parthenium hysterophorus</i> | – | 1.80 | 5.11 | – | 13.89 | – | – | – | 1.85 | – | – |
| <i>Phacelia artemisioides</i> | – | – | – | – | – | – | – | – | – | 1.08 | – |
| <i>Sphaeralcea miniata</i> | – | 0.57 | – | – | 2.50 | 1.67 | – | 1.92 | – | – | – |
| Shrubs | 4.76 | 2.78 | 0.79 | – | 43.27 | 6.85 | 2.00 | 9.26 | 85.35 | 2.36 | – |
| <i>Atriplex lampa</i> | – | – | – | – | 35.16 | – | – | – | 41.08 | – | – |
| <i>Junellia aspera</i> | 4.76 | – | – | – | 4.17 | 5.19 | 2.00 | – | 9.85 | – | – |
| <i>Larrea</i> spp. | – | – | – | – | 3.95 | – | – | 9.26 | 34.43 | 2.36 | – |
| <i>Lycium</i> spp. | – | 2.78 | 0.79 | – | – | 1.67 | – | – | – | – | – |
| Unidentified | – | 1.46 | – | – | – | – | – | – | – | – | – |
| Number of colonies | 1 | 5 | 4 | 1 | 4 | 3 | 2 | 4 | 3 | 3 | 4 |
| Total number of seeds | 21 | 486 | 382 | 38 | 62 | 51 | 45 | 47 | 44 | 90 | 103 |

included exclusively *S. ichu* seeds in the diet but *P. pronotalis* included high proportions of other species as well (Tables 1 and 2).

Diversity of all items in harvester ant diet decreased logarithmically with increasing seed abundance with a marked decline in diversity when seed abundance exceeded $1-6 \times 10^6$ seeds ha^{-1} (Fig. 5a,c,e). Linear regressions of diversity against $\log(\text{seed abundance})$ were significant for each species (*P. rastratus*: $H = 3.26-0.44 \log_{10}(\text{seeds ha}^{-1})$, $R^2 = 0.64$, $P = 0.005$; *P. pronotalis*: $H = 2.38-0.31 \log_{10}(\text{seeds ha}^{-1})$, $R^2 = 0.67$, $P = 0.002$; *P. inermis*: $H = 2.13-0.28 \log_{10}(\text{seeds ha}^{-1})$, $R^2 = 0.94$, $P < 0.001$). Diversity of seeds of different species in the diet, in contrast, was not associated with seed abundance for any ant species ($P > 0.05$; Fig. 5b,d,f).

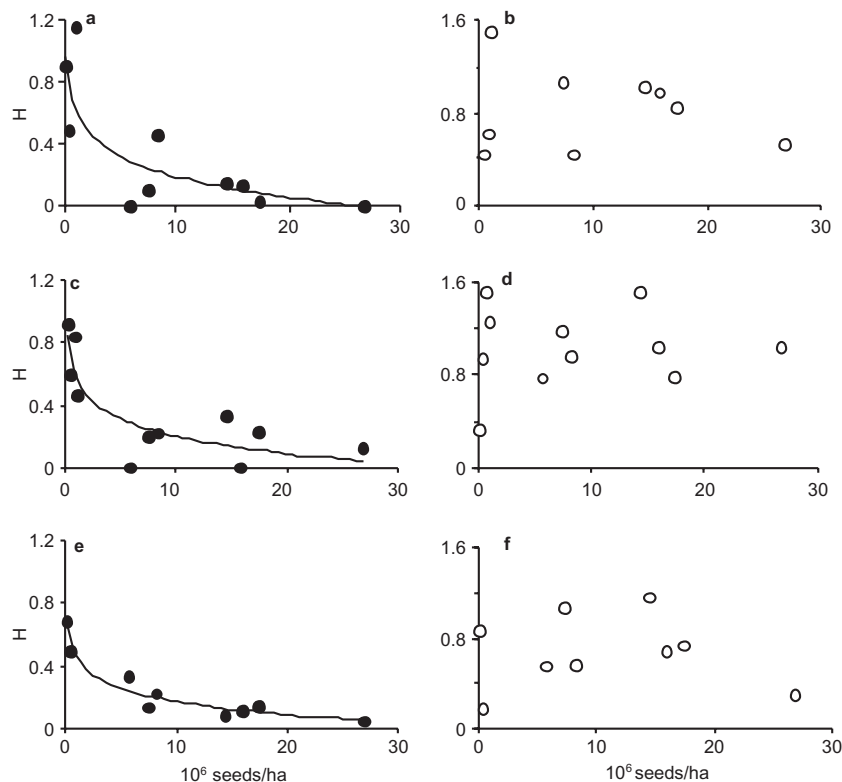
Percentage of the five most consumed seeds in *P. rastratus*' diet increased logarithmically with their abundance in the field (% in the diet = $-96.33 + 26.52 \log_{10}(\text{seeds ha}^{-1})$, $R^2 = 0.54$, $P = 0.015$; Fig. 6a). A similar pattern was observed for *P. pronotalis*, although with a marginally significant regression (% in the

diet = $-101.08 + 26.43 \log_{10}(\text{seeds ha}^{-1})$, $R^2 = 0.35$, $P = 0.053$; Fig. 6b). There seemed to be a threshold of seed abundance (again, between $1-6 \times 10^6$ seeds ha^{-1}) above which these two ant species collected almost exclusively the seeds of these five grasses. In contrast, the percentage of these seeds in the diet of *P. inermis* was always above 90%, showing no increasing trend (Fig. 6c).

Percentage in the diet of each of the most consumed species was not associated with relative abundance in the environment (most 95% confidence intervals for the concordance correlation coefficient did not approach 1; Fig. 7). The only exception was *Aristida* spp. for *P. inermis*, which was taken in proportion to its availability (confidence interval: $(-0.196, 0.934)$; Fig. 7). *Aristida* spp. was highly and positively selected by *P. rastratus* and *P. pronotalis*, *Pappophorum* spp. by the three species and *D. californica* by *P. inermis*, whereas the percentage of *T. crinita* and *S. ichu* in the diet of *P. pronotalis* and *P. inermis* was lower than that in the environment. There was also a positive selection for *D.*

Table 3. Mean percentage of seeds of different species in the diet of *Pogonomyrmex inermis* in October (O), December (D), February (F) and April (A) 2001–2002, 2002–2003 and 2003–2004 in the central Monte desert

| <i>Pogonomyrmex inermis</i> | 2001–2002 | | | | 2002–2003 | | 2003–2004 | | |
|----------------------------------|-----------|-------|-------|-------|-----------|-------|-----------|-------|-------|
| | O | D | F | A | F | A | D | F | A |
| Grasses | 100 | 100 | 97.41 | 98.76 | 99.94 | 99.85 | 100 | 99.89 | 100 |
| <i>Aristida</i> spp. | – | 1.26 | 22.27 | 10.21 | 16.02 | 3.54 | – | 3.26 | 0.86 |
| <i>Trichloris crinita</i> | 7.14 | 36.79 | 12.20 | 17.19 | 30.72 | 15.10 | 3.33 | 16.61 | 3.45 |
| <i>Pappophorum</i> spp. | 42.86 | 8.65 | 17.73 | 1.92 | 14.98 | 70.48 | 88.33 | 44.84 | – |
| <i>Digitaria californica</i> | 50.00 | 0.32 | 38.43 | 67.87 | 17.57 | 2.57 | – | 30.95 | 86.07 |
| <i>Stipa ichu</i> | – | 49.80 | 2.58 | 0.44 | 20.60 | 8.10 | 8.33 | 0.88 | – |
| <i>Setaria leucopila</i> | – | 1.28 | 0.51 | – | 0.06 | – | – | – | – |
| <i>Sporobolus cryptandrus</i> | – | – | 0.91 | – | – | – | – | – | – |
| <i>Chloris castilloana</i> | – | – | 2.78 | 1.14 | – | 0.05 | – | – | – |
| <i>Schismus barbatus</i> | – | 1.89 | – | – | – | – | – | – | – |
| <i>Neobouteloua lophostachya</i> | – | – | – | – | – | – | – | 3.34 | 9.62 |
| Forbs | – | – | 2.47 | 0.88 | 0.06 | 0.15 | – | 0.11 | – |
| Asteraceae 1 | – | – | 0.08 | – | – | – | – | – | – |
| <i>Conyza</i> spp. | – | – | 2.20 | 0.88 | 0.06 | – | – | – | – |
| <i>Cryptandra mendocina</i> | – | – | 0.06 | – | – | – | – | 0.11 | – |
| <i>Lappula redowski</i> | – | – | 0.13 | – | – | – | – | – | – |
| <i>Sphaeralcea miniata</i> | – | – | – | – | – | 0.10 | – | – | – |
| <i>Parthenium hysterophorus</i> | – | – | – | – | – | 0.05 | – | – | – |
| Unidentified | – | – | 0.13 | 0.37 | – | – | – | – | – |
| Number of colonies | 1 | 2 | 5 | 5 | 3 | 3 | 3 | 6 | 4 |
| Total number of seeds | 14 | 209 | 735 | 512 | 1889 | 1307 | 37 | 1484 | 104 |

**Fig. 5.** Mean diversity (H: Shannon–Wiener diversity index) of items (black) and seed species (white), in the diet of (a,b) *P. rastratus*, (c,d) *P. pronotalis* and (e,f) *P. inermis* on each sampling occasion as a function of total seed abundance of the five most consumed species. Significant logarithmic regression curves are shown as full ($P < 0.05$).

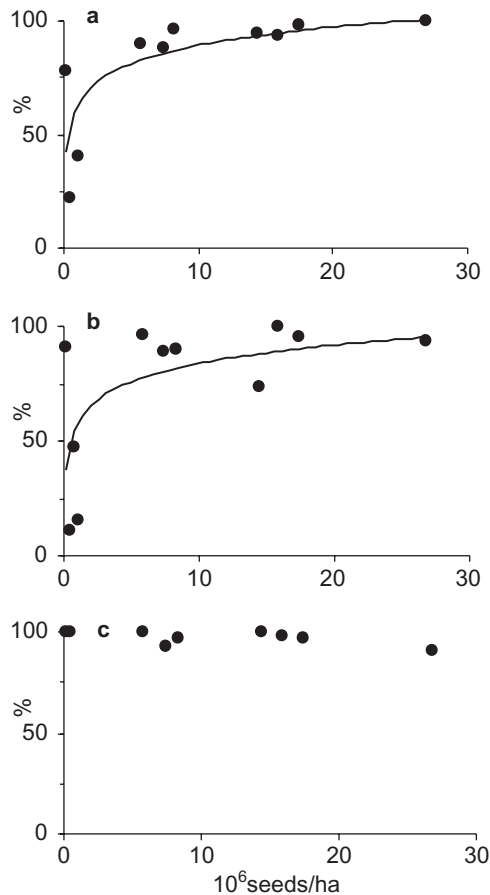


Fig. 6. Mean percentage of the five most consumed seeds (the grasses *Aristida* spp., *Trichloris crinita*, *Pappophorum* spp., *Digitaria californica* and *Stipa ichu*) in the diet of (a) *P. rastratus*, (b) *P. pronotalis* and (c) *P. inermis* on each sampling occasion as a function of their abundance in the field. Significant ($P < 0.05$) or marginally significant regression curves are shown.

californica by *P. rastratus* and *P. pronotalis* and a negative selection for *S. ichu* by *P. inermis* although less marked than in the other cases (Fig. 7). *Trichloris crinita* was positively, negatively or not selected by *P. rastratus* on different occasions.

DISCUSSION

Although *P. rastratus*, *P. pronotalis* and *P. inermis* are highly specialized in seed collection, their diet was more generalist (including a higher percentage of invertebrates, vegetative plant parts and other items) when seed abundance of the most consumed species was low, as predicted by the classic 'diet' model of foraging theory (Schoener 1971; Stephens & Krebs 1986). *Messor pergandei* showed a similar trend in the Sonoran desert, carrying a higher proportion of insects and a lower proportion of seeds during a drought than

in a wetter period with higher seed abundance (Tevis 1958). The diversity of items in the diet decreased logarithmically with increasing seed abundance for the three studied species, suggesting that the foraging efficiency of the ants allows them to rely on seeds exclusively above certain levels of seed abundance. A higher search time and a corresponding decrease in their foraging efficiency may force them to switch to less-preferred items at low seed abundance (Davidson 1977; Traniello 1989). However, diversity of seeds of different species in the diet was not related to grass seed abundance in spite of the important temporal changes in seed composition in the environment. Ants always included several species in their diet, with alternating prevalence, resulting in no detectable trend in seed diversity in the diet.

Seeds of the most consumed species, *Aristida* spp., *Pappophorum* spp., *T. crinita*, *D. californica* and *S. ichu*, increased their proportion in the diet of *P. rastratus* and *P. pronotalis* as their abundance increased in the field. This association was logarithmic, implying that small changes in seed abundance at low levels caused proportionally greater changes in the proportion in the diet than at higher levels. Although foraging rates were not measured directly, the response of these ants to grass seeds can still be interpreted as Type 3 functional responses (Holling 1959), as at low seed abundance the foraging activity is also lower, resulting in very low consumption rates and leading to a sigmoidal rather than to an hyperbolic function of a Type 2 functional response (Holling 1959). Also, in a Type 3 functional response the proportion of food types in the diet is expected to increase with their abundance in the environment, as was found for *P. rastratus* and *P. pronotalis*, whereas in a Type 2 response this proportion should decrease (Juliano 2001). Type 3 responses in the context of a real community can be generated by switching on the part of the consumer (i.e. they forage on alternative food types when the main type is scarce), by an increase in searching efficiency or a decrease in its handling time with increasing food density (Begon *et al.* 1996). In fact, these ants forage on alternative seed types when grass seeds are scarce (i.e. forbs and shrub seeds) and their foraging efficiency probably increases at higher seed abundance by promoting recruitment of foragers to seed patches (increasing searching efficiency by decreasing search time; Davidson 1977; Traniello 1989). Under a Type 3 functional response, the potential for predators to deplete a resource is reduced considerably compared with a Type 2 response where the proportion of prey consumed is still high at low levels of prey availability (Hassell 1978). Thus, the expected top-down effects of *P. rastratus* and *P. pronotalis* on grass seed abundance would be attenuated as a result of this particular functional response.

In contrast to what was observed for *P. rastratus* and *P. pronotalis*, the proportion of seeds of the five grass

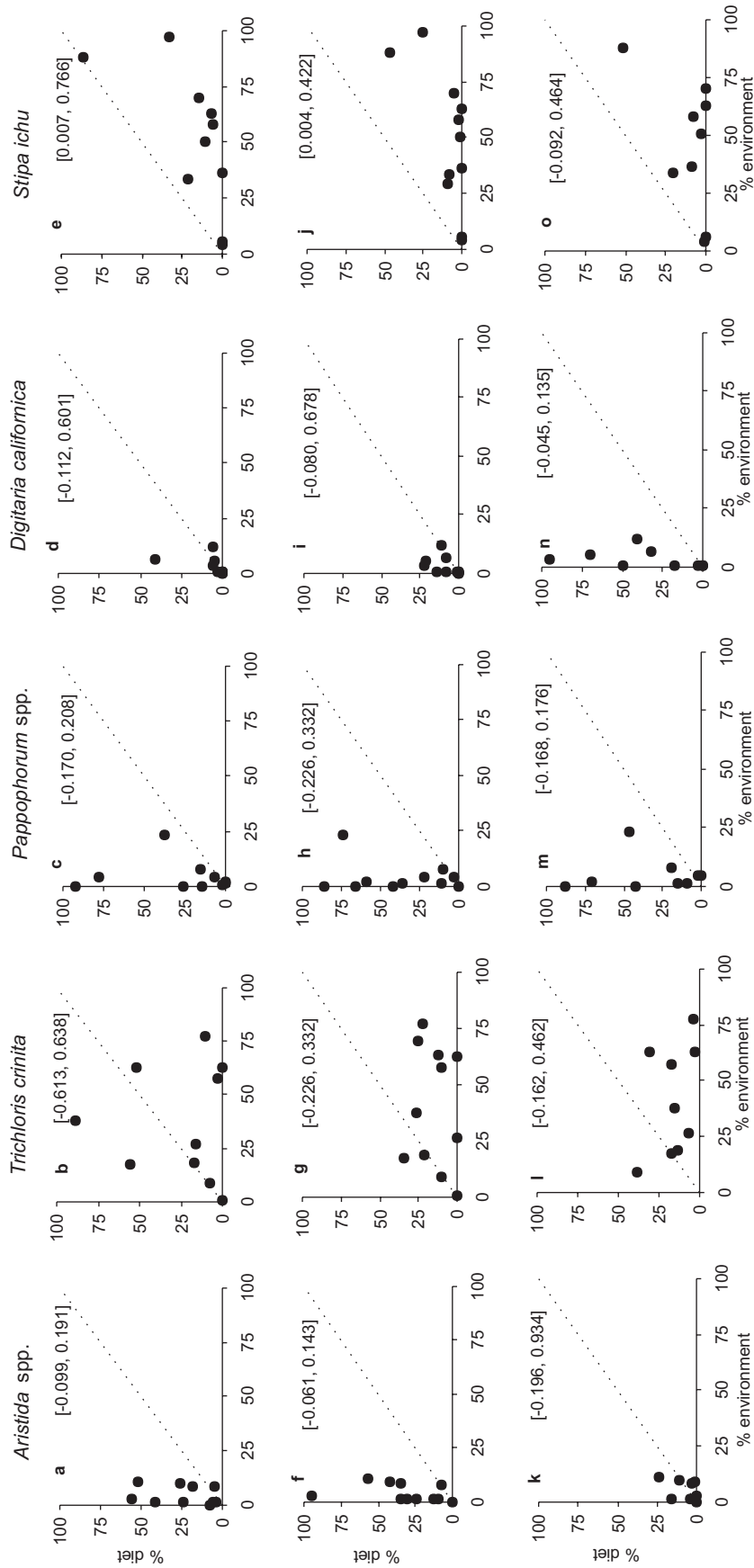


Fig. 7. Mean percentage of the most consumed seeds in the diet of (a–e) *P. rastrospus*, (f–j) *P. pronotalis* and (k–o) *P. inermis* as a function their percentage in the environment on each sampling occasion. Discontinuous lines represent linear curves of slope b = 1. Limits of 95% confidence interval for the concordance correlation coefficient are shown.

species in the diet of *P. inermis* was always very high, independent of seed abundance in the environment. Colonies of *P. inermis* displayed very low external activity during sampling occasions when these seeds were scarce. Although in this habitat soil temperature is temporally correlated both with low seed abundance and low ant activity at the beginning of the season, *P. inermis* also showed low activity levels on those mid-season occasions when soil temperature was high enough but abundance of grass seeds was still low due to scarce rain (e.g. December 2002, when *P. rastratus* and *P. pronotalis* were already foraging actively). The more restricted diet of *P. inermis* could lead to a lower return rate of loaded foragers when grass seeds are scarce in their search area, resulting in a negative feedback that decreases the general foraging activity of the colony (as experimentally demonstrated for *P. barbatus*; Gordon 1991). A large decrease in ant activity associated with scarcity of preferred food items has also been observed in the harvester ants *P. rugosus* and *M. pergandei* in Arizona (Mehlhop & Scott 1983). Although the response of *P. inermis* at low levels of seed abundance differs from that of *P. rastratus* and *P. pronotalis*, its predicted effect on resources was similar: an attenuation of top-down effects.

Among grasses, relative abundance of the most consumed seeds did not influence their proportion in the diet. Overall, *Pappophorum* spp., *D. californica* and *Aristida* spp. were positively selected and thus, they would be the most affected species by ant predation. However, as already mentioned, the flexibility in the diet of *P. pronotalis* and *P. rastratus* and the low foraging activity of *P. inermis* during periods of low resource abundance could attenuate this effect. Detailed studies of total seeds harvested in relation to total seed abundance need to be performed throughout the activity season of the ants to estimate the proportion of total seeds removed and to determine the most vulnerable periods.

In summary, the diet and foraging activity of the three *Pogonomyrmex* species varied with resource abundance. Although the three species mainly consumed grass seeds, which are produced even during droughts (Kemp 1989; R. Pol, G. Pirk & L. Marone, unpubl. data), ant activity season also included periods of low grass seed abundance. *Pogonomyrmex pronotalis* and *P. rastratus* diets were flexible enough to maintain their external foraging activity levels during these periods. Seeds stored in granaries could act as 'buffers' (Reyes-López & Fernández-Haeger 2002) to sustain the internal activities of the colonies (e.g. reproduction, maintenance and brood feeding) while seed collecting is scarce. Seed storage could especially benefit species with more selective diets, such as *P. inermis*, that restricted its foraging activity to high resource periods. It is important to note that because of its more constant diet and higher dependence on grass seeds, *P.*

inermis could actually be the species displaying the greatest response to low resource levels, not through changing its diet but by minimizing its levels of foraging activity.

The simultaneous study of the temporal dynamics of the diet together with that of resource abundance and composition allowed us to assess the importance of resource levels on consumers. An inflexible pattern of consumption in a system where resources are temporally scarce would result in greater potential for top-down effects of ants on seeds (Crist & MacMahon 1992). However, our results indicate the relevance of bottom-up effects and the attenuation of the expected top-down effects at low seed abundance through ants remaining relatively flexible in their diet and foraging activity patterns. Thus, bottom-up effects should be taken into account when predicting and evaluating the effects of ants on seed resources.

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