

## Foraging strategies and foraging plasticity in harvester ants (*Pogonomyrmex* spp., Hymenoptera: Formicidae) of the central Monte desert, Argentina

Rodrigo G. POL, Javier LOPEZ DE CASENAVE & Fernando A. MILESI



### Abstract

Foraging strategy determines the way harvester ants use space and therefore their access and impact on seed resources. In this study, we described the foraging strategy of three sympatric South American species of *Pogonomyrmex* ants to confirm that they are solitary foragers as is suggested anecdotally in the literature. Then we tested whether those foraging strategies are fixed or flexible in response to seed density and distribution. Based on individual and group movements of foraging ants, we determined that *P. rastratus* MAYR, 1868 is exclusively a solitary foraging species, *P. inermis* FOREL, 1914 use a group-foraging strategy with limited recruitment, and *P. mendozanus* CUEZZO & CLAVER, 2009 displays an intermediate foraging system in which workers are typically solitary foragers but also recruit nestmates to high-density seed patches. The addition of seeds near the nest modified the foraging behavior of the three species by different amounts. Individual foragers of each species reduced their search time and search area, and colonies increased their foraging activity rate, probably as a result of a higher returning rate of successful foragers after seed addition. Such behavioral responses were much more conspicuous in *P. mendozanus* than in the other two species. Flexibility in foraging and diet breadth reported for some of these harvester ants may constitute important adaptive features in the central Monte desert where seed abundance is highly heterogeneous, irregular, and severely affected by anthropic disturbances.

**Key words:** Foraging behavior, seed availability, granivory, harvester ants, *Pogonomyrmex*, Monte desert.

Myrmecol. News 21: 1-12

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 9 January 2014; revision received 14 May 2014; accepted 20 May 2014

Subject Editor: Bernhard Ronacher

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### Introduction

Harvester ants are widely recognized as important seed consumers in arid and semiarid areas around the world (BROWN & al. 1979, HÖLLDOBLER & WILSON 1990, MACMAHON & al. 2000). They can remove large numbers of seeds, with particularly high impacts on preferred species (WHITFORD 1978, REICHMAN 1979, CRIST & MACMAHON 1992, PIRK & LOPEZ DE CASENAVE 2006). Their foraging may affect the relative abundance and spatial distribution of species in the soil seed bank (WHITFORD 1978, CRIST & MACMAHON 1992, MULL & MACMAHON 1996, AVGAR & al. 2008, ARNAN & al. 2010), which can ultimately have consequences on the structure of plant communities (INOUE & al. 1980, SAMSON & al. 1992, ESPIGARES & LÓPEZ-PINTOR 2005).

The effects of seed harvesting by ants depend on the temporal and spatial patterns of seed collection that determine when, where, and which seeds are consumed (CRIST & MACMAHON 1992). The spatial pattern of seed predation by harvester ants is highly associated with their foraging

strategy. It may range from solitary harvesting without any cooperation during search and food retrieval to various levels of cooperative foraging and recruitment among nestmates (TRANIELLO 1989, HÖLLDOBLER & WILSON 1990, JOHNSON 2000, RETANA & al. 2004, ARNAN & al. 2010, PLOWES & al. 2013). In group-foraging species, workers depart from the nest in a column or along a well-defined trail and break off to forage at the distal end of the column. Workers actively recruit nestmates to seed patches, thus facilitating rapid harvest of localized resources. In contrast, workers of solitary-foraging species radiate out from the nest in almost all directions, spend more time searching for seeds, and exhibit poor nestmate recruitment (JOHNSON 2000, PLOWES & al. 2013). Experimental and theoretical studies have shown that group-foragers find and exploit clumped and abundant resources more efficiently, whereas solitary foragers are more efficient when resources are scattered and sparse (DAVIDSON 1977, JOHNSON & al. 1987, JAFFE & DENEUBOURG 1992, but see FLANAGAN &

al. 2012). Harvester ant species usually show only one of those foraging strategies, but some species can display an intermediate foraging method in which workers are typically solitary foragers but recruit nestmates when high-density food patches are found (although at a slower rate than typical group-foragers; HÖLLDOBLER 1976, DAVIDSON 1977, HAHN & MASCHWITZ 1985, JOHNSON 2000). This flexible foraging strategy can be more efficient in environments with a high spatio-temporal variability in density of food resources (HAHN & MASCHWITZ 1985, LANAN 2014).

The genus *Pogonomyrmex* comprises about 60 species of harvester ants of open habitats, often arid, from Patagonia to south-western Canada (TABER 1998). They have been extensively studied in North American deserts, of which they are a dominant feature (MACKAY 1991, MACMAHON & al. 2000, JOHNSON 2000, 2001), though phylogenetic reconstructions suggest a South American origin for the genus (TABER 1998). Whereas some North American species exhibit group foraging (which is a derived character) by recruiting nestmates with trail pheromones (HÖLLDOBLER & al. 2001, JOHNSON 2001), South American *Pogonomyrmex* species are allegedly exclusively solitary-foragers (KUSNESOV 1951, 1963, TABER 1998), though this claim is mostly based on anecdotal field observations. Laboratory studies on *Pogonomyrmex vermiculatus* EMERY, 1906 (a Chilean species) proved them able to produce, detect, and use trail pheromones to recruit foragers which improved the foraging success of the colony (TORRES-CONTRERAS & al. 2007, TORRES-CONTRERAS & NIEMEYER 2009). However, there are still no field studies on the individual or group movements of foraging ants of the South American *Pogonomyrmex* species and thus no evidence of which foraging strategies are used in natural conditions.

*Pogonomyrmex rastratus* MAYR, 1868, *P. mendozanus* CUEZZO & CLAVER, 2009, and *P. inermis* FOREL, 1914 (Hymenoptera: Formicidae) are three sympatric harvester ant species coexisting in the central Monte desert of Argentina (PIRK & al. 2004). They all forage mostly for grass seeds from spring to autumn (POL & LOPEZ DE CASENAVE 2004, PIRK & LOPEZ DE CASENAVE 2006). Their relatively high rate of seed removal during spring and summer suggests a potential effect on soil seed bank composition, especially on preferred grasses (PIRK & LOPEZ DE CASENAVE 2006). In this study we describe the foraging strategy of the three species in field conditions at the Biosphere Reserve of Ñacuñán (Mendoza, Argentina) to confirm if they are solitary foragers as previously asserted. We also evaluate the hypothesis of a flexible foraging strategy, i.e., whether the foraging strategy of these ants changes according to fluctuations in grass seed density and the spatial aggregation of seeds. We test the specific prediction that an experimental increase in local density of the most consumed and preferred grass seeds will promote change towards a group-foraging strategy.

## Methods

### Study area

The Biosphere Reserve of Ñacuñán (34° 03' S-67° 54' W) is located in the central portion of the Monte desert, Mendoza Province, Argentina. The main habitat is the algarrobal, an open woodland where *Prosopis flexuosa* and *Geof-*

*froea decorticans* trees are scattered within a matrix of perennial tall shrubs (mostly *Larrea divaricata*, but also *Condalia microphylla*, *Capparis atamisquea*, *Atriplex lampa*, and *Larrea cuneifolia*), low shrubs (*Lycium* spp., *Mulgoraea aspera*, and *Acantholippia seriphoides*), and perennial grasses (e.g., *Trichloris crinita*, *Pappophorum* spp., *Sporobolus cryptandrus*, *Aristida* spp., *Digitaria californica*, *Setaria leucopila*, and *Jarava ichu*). The Forb cover (e.g., *Chenopodium papulosum*, *Phacelia artemisioides*, and *Parthenium hysterophorus*) is highly variable from year to year. *Pogonomyrmex* colonies are frequent on and near the dirt roads that cross the Ñacuñán Reserve (PIRK & al. 2004). Most of them are approx. 6 m wide and support infrequent foot, horse, and vehicle traffic. They have lower vegetation cover than the surrounding habitats (woody plants are removed periodically) and their compacted surface results in much more exposure to sun, rain and wind. Ñacuñán's climate is dry and highly seasonal. Mean annual temperature is 15.9°C and mean annual rainfall is 342 mm with high inter-annual variation (range: 91 - 585 mm; 1972 - 2004); ~ 75% of the rainfall occurs in spring and summer (October - March).

### Foraging strategies

We described the foraging strategy of the three *Pogonomyrmex* species in colonies located in two structurally distinct habitats: within the open woodland and on the dirt roads. During summer 2003 - 2004, we mapped the foraging trails of eight to twelve ants from each of seven colonies per species (*P. rastratus*, *P. mendozanus* and *P. inermis*), three located in the open woodland and four on the roads. Single focal ants were followed since leaving the nest, and their positions marked with toothpicks, usually every 30 seconds, until food items were collected and they start returning to the nest. Foragers that did not collect food were not considered further. Successfully tracked workers were stained with fluorescent powder or momentarily removed from the colony to record only one track per individual ant. To map the foraging trips, the whole area encompassed by the foragers of a colony was gridded (1 m<sup>2</sup> squares) and photographed with a digital camera fixed on a 3 m vertical aluminum pole. We used distinctively colored toothpicks and small paper shapes to recognize individual trajectories. For every studied colony, a mosaic of 31 - 96 images was assembled to compile a map that included the nest entrance and the foraging paths.

We considered each individual foraging trip as consisting of two phases: 1) Traveling, during which the worker moves away from the nest at a relatively high speed towards the area where it searches for seeds; and 2) searching, during which the worker turns frequently, walks at a slower pace on a convoluted path, and probes and handles items on the ground (TRANIELLO 1989, CRIST & MACMAHON 1991). The switch between traveling and searching behavior was clearly detectable at field. We measured the time used by each ant in each of these foraging phases. The area explored by ants during the search phase was estimated by the minimum convex polygon (JENRICH & TURNER 1969) that encompassed all the marks along the path. To determine if foragers employed different or shared travel areas (i.e., trails) we measured the overlap between pairs of individual foraging paths, assuming each path as 50 cm wide (CRIST & MACMAHON 1991). If the

overlapping area between paths was > 70% we considered them as sharing a single trail. We then calculated the number of simultaneous foraging trails per colony from the eight to twelve ant paths mapped.

Additionally, we estimated the foraging activity rate of each colony and the outbound directions of the foragers from video records of 50 - 70 foragers leaving each nest (in one colony only 31 foragers were recorded). We fitted a wire ring around the nest entrance that had a diameter of 50 cm and graduations every 5° and was supported by three small wire legs, and mounted a video camera on top with the help of a tripod.

### Seed bait experiment: plasticity of foraging strategies

According to our hypothesis, foraging strategies in these harvester ants are flexible and change according to grass seed density. If this is true we expect the colonies to show an individual foraging strategy when seeds are scarce and scattered, but shift to a more cooperative system when grass seed density increases locally. When seed density is relatively low, seeds are sparse and individual foraging dominates, we expect the workers to radiate out from the nest in almost all directions, using different or rarely used trails, and to spend more time searching for food, covering extensive areas. On the other hand, if abundant and concentrated sources of seeds are available (e.g., experimentally supplied) we expect foragers to recruit nestmates along shared, well-defined trails (e.g., foraging columns or trunk-trails) in a few directions, and to show reduced search times and areas. Since group foraging behavior involves an active recruitment of nestmates, we also expect an increase of foraging activity in the colony when seed density is high.

To test those predictions we carried out seed manipulation experiments on the four colonies of each species located on the roads. Foraging strategies were very similar among colonies in the open woodland and on the roads (see Results) and it was easier to evaluate the experimental results in this habitat (with less physical obstacles potentially restricting ant movements). Following the previously described procedure, we mapped 8 - 13 (mean = 10.3) successful foraging trips per colony, recorded the outgoing directions of > 50 workers and estimated the foraging activity rate of each colony both before and after experimental seed addition near the nest. Two bait stations were placed in different quadrants (i.e., 90 - 180° apart) 3 - 4 m around each nest entrance (the mean foraging distance recorded for these species; > 80% of foraging events occur within a ~ 7 m circle around their nests; POL & al. 2011) in areas which were not being intensively exploited by foragers at the moment (i.e., with low frequency of outgoing direction taken by foragers, and < 2 mapped foraging paths recorded before seed addition). We avoided microhabitats that restricted ant movements or prevented our observation (e.g., beneath the cover of dense shrubs and trees). At each bait station (an area of approximately 0.06 m<sup>2</sup>) we added recently collected propagules of the most consumed and preferred native grasses (i.e., *Aristida* spp., *T. crinita*, *D. californica*, *Setaria* spp., *Pappophorum* spp., and *J. ichu*; PIRK & LOPEZ DE CASENAVE 2006, PIRK & al. 2009) on the ground and on their spikes (fixed to a piece of buried cardboard). Baits were checked twice a day and seeds and spikes replenished as required. To reduce the effect of soil tem-

perature and wind on colony activity and workers' foraging behavior, all measurements were taken on sunny and windless summer days during periods of maximum foraging activity (i.e., 09:00 - 11:00 and 17:00 - 20:00; see POL & LOPEZ DE CASENAVE 2004).

Outgoing directions of foragers corresponded well to the orientation of mapped individual travel trajectories (see Results) and were much easier to record. In order to increase the evidence of the effects of seed addition, we further recorded the outgoing directions of foragers near the nest entrance before and after seed addition (following the previously described protocol) in another two *Pogonomyrmex rastratus*, six *P. inermis* and three *P. mendozanus* colonies. In total, six, ten, and seven colonies of *P. rastratus*, *P. inermis* and *P. mendozanus* were sampled, respectively.

### Statistical analyses

Rayleigh tests were performed to assess whether the outbound directions of foragers depart from a uniform distribution (BATSCHELET 1981), which is the prediction for an individual foraging strategy with no recruitment (and no physical restrictions to movement at ground level). We also estimated the mean vector length ( $r$ ) of that distribution, ranging between 0 (uniform distribution) and 1 (perfectly directional). Distribution of outgoing directions of foragers before and after seed bait experiment was compared using Watson's U<sup>2</sup> Test (BATSCHELET 1981). Circular statistics were performed using Oriana 4 program (KOVACH 2012).

For tests based on one value per colony (number of trails, mean vector length) we used two-way factorial ANOVA (Habitat × Spp) to assess differences among the three species in the open woodland and on dirt roads. ANOVA assumptions were assessed graphically following QUINN & KEOUGH (2002). The Kramer modification of Tukey's test (DAY & QUINN 1989) was used for a posteriori multiple comparisons. For tests based on one data value per ant (search time, foraging area, travel time) we used random intercepts linear mixed models to account for the hierarchical structure of the dataset (ants nested within colonies), including Spp as a fixed factor and Colony as a random grouping factor nested within Spp. Measured variables were log-transformed in order to assume normality of the residuals, which was graphically checked (qqplots, scatterplots and boxplots of residuals against predicted values).

To analyze the results of the experiments of seed addition we further included Experiment as a two-level fixed factor (within-colonies), potentially interacting with the fixed factor Spp (i.e., a fixed interaction term) or with the random factor Colony (i.e., a random intercept and slope mixed model). In the case of a single integrative value at the colony level (nest activity) this results in a repeated-measures or split-plot design (with Spp as between-colonies and Experiment as within-colonies), which was also analyzed as a general mixed model. When variances among ants within colonies or among colonies within species resulted heterogeneous among groups or were affected by the experimental treatment, they were modeled accordingly.

Search time and foraging area per ant were strongly correlated in every species (Pearson correlation in log-log scale: *P. inermis*:  $r = 0.738$ ,  $P < 0.001$ ,  $N = 32$ ; *P.*

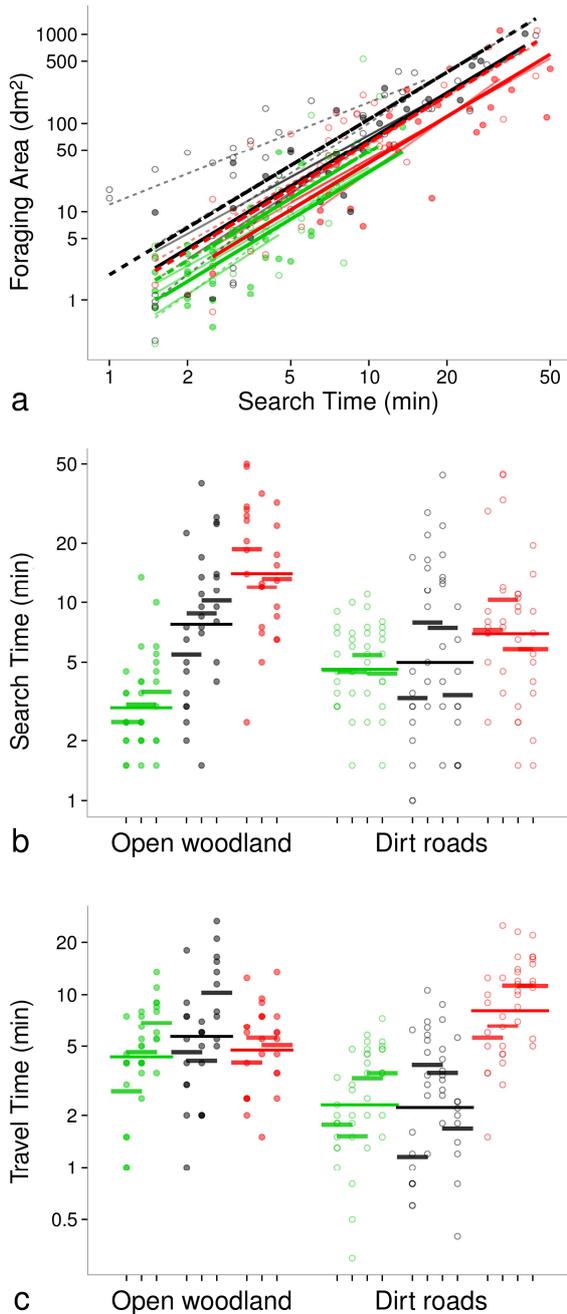


Fig. 1: Main characteristics of the individual foraging paths of *Pogonomyrmex inermis* (green), *P. mendozanus* (black), and *P. rastratus* (red) harvesting ants in two habitats in the central Monte desert. Note that all continuous axes are logarithmic scales. (a) Log-log relationships between foraging search area and search time of individual paths of workers from colonies of the three species located in the open woodland (solid lines, with filled circles for individual ants) and on dirt roads (dashed lines and open circles). (b - c) Time spent searching and traveling by individual foragers from colonies in the open woodland and on dirt roads, with estimated means per colony (short segments) and per species (long segments). Three and four colonies of each species were sampled in the open woodland and on dirt roads, respectively. The number of workers sampled on each habitat was: *P. inermis* N = 32 + 39; *P. mendozanus* N = 29 + 40; *P. rastratus* N = 27 + 37. See detailed results of linear mixed models in text.

*mendozanus*:  $r = 0.875$ ,  $P < 0.001$ ,  $N = 29$ ; *P. rastratus*:  $r = 0.827$ ,  $P < 0.001$ ,  $N = 27$ ), as previously reported in other harvester ants (CRIST & MACMAHON 1991). We used a linear mixed model to test for a linear relationship in log-log scale between search time and foraging area, allowing for different random slopes and intercepts per colony (e.g., individual foraging efficiency affected by different seed availability and aggregation of seeds around its colony), and testing for all fixed factor interactions (different slopes and intercepts among Spp  $\times$  Habitat combinations).

All mixed models were analyzed using the nlme package (PINHEIRO & BATES 2000, PINHEIRO & al. 2012) within R (R CORE TEAM 2012) running on RStudio Desktop for Linux (RSTUDIO 2012). We followed the general top-down modeling approach suggested by ZUUR & al. (2009), first selecting the (optimal) random structure (constrained by experimental design) for saturated fixed models and then comparing nested models trying to simplify the fixed structure for unsupported parameters by deleting explanatory variables. The depleted (simpler) model was compared at each simplifying step with the reference (full) model based on Akaike's information criterion (AIC) and likelihood ratio tests (L), estimated by Restricted Maximum Likelihood (REML; for tests of random factors between models with the same fixed structure) or by Maximum Likelihood (ML; for tests of fixed factors between models with the same random structure). The difference of AIC values between the reduced and reference model ( $\Delta$ AIC) is reported, as well as the likelihood ratio tests with their associated degrees of freedom (difference in number of parameters between the models) and corresponding p-value. Small  $\Delta$ AIC, low L and high p-value suggest model simplification (i.e., not enough empirical support to sustain the more complex model). Parameters of final models reported were estimated by REML.

## Results

### Individual search time and foraging area

The log of area that an individual forager searched for an item during a foraging trip was strongly and positively related with the log of time it spent searching (Fig. 1a). In mixed models allowing for inter-colony variability (random intercepts and slopes), we were not able to detect any relevant interaction term between the fixed factors Spp, Habitat and Search Time (deletion tests of: Habitat  $\times$  Spp  $\times$  Search Time:  $\Delta$ AIC = -2.55;  $L_2 = 1.45$ ,  $P = 0.484$ ; Habitat  $\times$  Search Time and Spp  $\times$  Search Time:  $\Delta$ AIC = -5.23;  $L_3 = 0.77$ ,  $P = 0.857$ ; Habitat  $\times$  Spp:  $\Delta$ AIC = -1.47;  $L_2 = 2.53$ ,  $P = 0.281$ ). The more parsimonious model to account for the available data of individual foraging areas involved a single population-level slope given by the continuous predictor Search Time ( $\Delta$ AIC = 57.32;  $L_1 = 59.32$ ,  $P < 0.001$ ), with both Spp ( $\Delta$ AIC = 9.45;  $L_3 = 13.45$ ,  $P = 0.001$ ) and Habitat ( $\Delta$ AIC = 7.71;  $L_1 = 9.71$ ,  $P = 0.002$ ) as additive factors. According to this model, search area increases with search time ( $\beta = 1.755$ ,  $SD = 0.107$ ) and, for a given search time, ants of colonies located on dirt roads (of any species) searched within a bigger polygon ( $\beta_{roads} = 0.233$ ,  $SD = 0.074$ ) than colonies in the open woodland, while *Pogonomyrmex mendozanus* workers searched faster or over a less convoluted path ( $\beta_{PM} =$

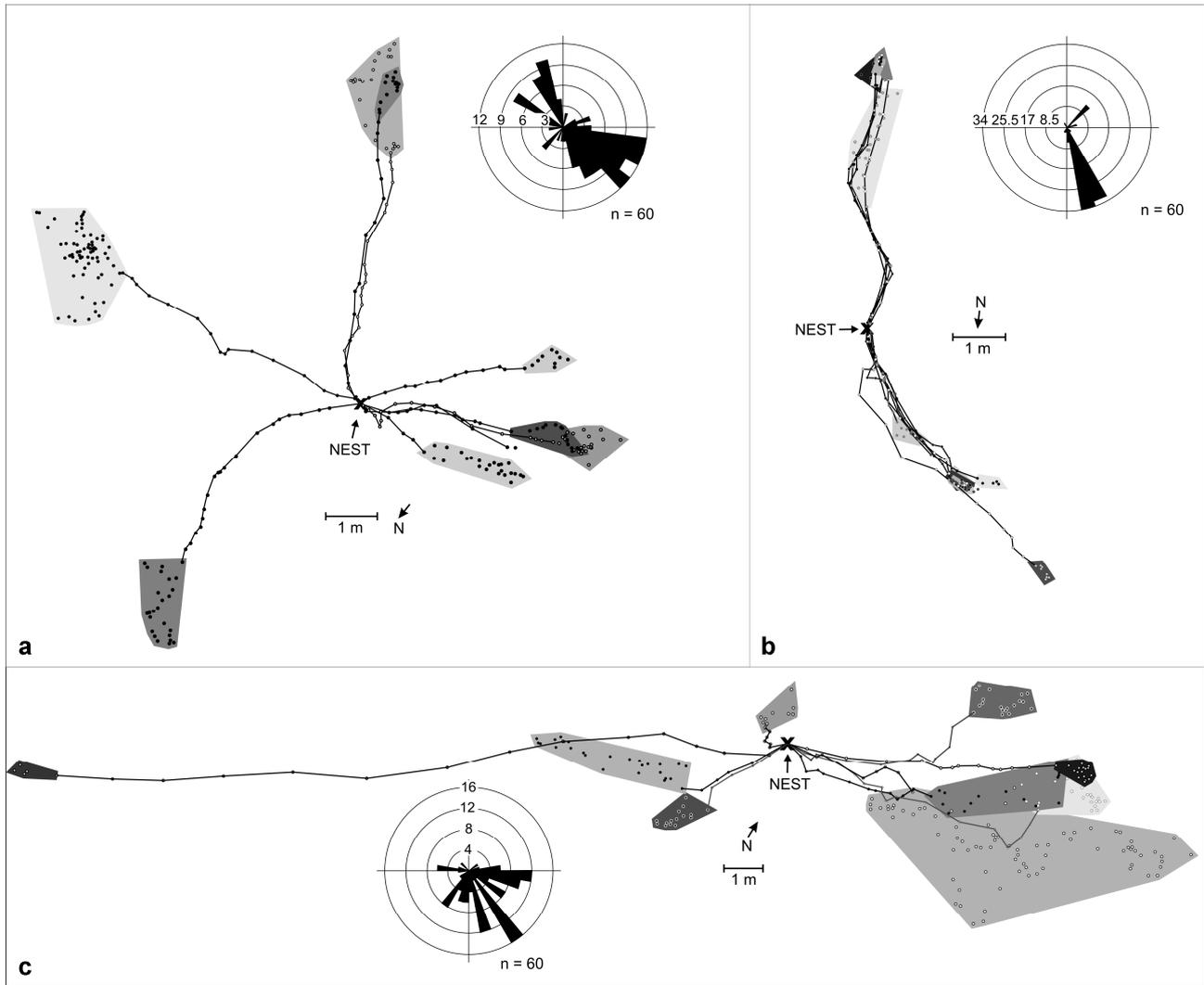


Fig. 2: Maps showing the spatial foraging patterns of workers from typical colonies of *Pogonomyrmex rastratus* (a), *P. inermis* (b), and *P. mendozanus* (c) located in the open woodland in the central Monte desert (maps of additional sampled colonies in Appendices S1 - S3). Individual travel trajectories are represented with small dots (which indicate the position of a focal ant every ~ 30 sec) and lines departing from nest entrance (X), and the search area by grayscale polygons at the distal end of travel trajectories. Circular histogram graph shows the frequencies and distribution of the outgoing directions taken by 60 foragers leaving the nest. Map and circular graph are oriented in the same direction relative to North.

0.369, SD = 0.107,  $t = 3.45$ ,  $P = 0.003$ ) than workers of *P. inermis* (reference level) and *P. rastratus* ( $\beta_{PR} = 0.105$ , SD = 0.107,  $t = 0.98$ ,  $P = 0.340$ ) in both habitats (though foraging times do not necessarily overlap among the three species, see below). As a consequence of this direct proportionality between individual foraging area and search time, for the sake of simplicity the following results are only those based on time.

### Foraging strategies

The mean time (in log scale) that an individual harvester ant searched for food on the ground differed among species and habitats (Fig. 1b). Intra-colony variation in search time was ~ 40% lower in *Pogonomyrmex inermis* than in the other two species (heterogeneous variances per Spp vs. homogeneous variances:  $\Delta AIC = 9.84$ ,  $L_2 = 13.84$ ,  $P < 0.001$ ). The more parsimonious model suggests the inclusion of a relevant interaction term between Habitat and

Spp ( $\Delta AIC = 4.86$ ,  $L_2 = 8.86$ ,  $P = 0.012$ ): while those species with a higher mean search time in the open woodland (*P. rastratus*: 14.55 min; *P. mendozanus*: 8.01 min) searched faster when in colonies located on the roads (7.19 min less and 5.15 min less, respectively), *P. inermis*, though always the fastest species, shows the opposite trend (3.06 min in open woodland, 4.77 min on roads). In consequence, the difference in mean search time among species is higher in the open woodland than on the roads (Fig. 1b).

There was much more variation in search time among ants within colonies than mean values compared across colonies (intra-class correlations: 0.07 in *Pogonomyrmex inermis* to 0.16 in *P. mendozanus*). This high variation within a colony agrees with the observation that foraging areas usually did not overlap between sampled nestmates in *P. rastratus* and *P. mendozanus* (Figs. 2a, c, and Appendices S1 and S2, as digital supplementary material to this article at the journal's web page). In contrast, workers of

*P. inermis* searched for seeds in very small areas, usually near a grass, that were simultaneously exploited by most other foragers in the colony (Fig. 2b, Appendix S3).

Travel times, on the other hand, showed homogeneous intra-colony variations among species and habitats, with a higher proportion of variation explained at the colony level (intraclass correlation: 0.40). There was a relevant Spp  $\times$  Habitat interaction term ( $\Delta\text{AIC} = 4.85$ ,  $L_2 = 8.85$ ,  $P = 0.012$ ), but the general pattern was almost the opposite of search times: the three species showed similar mean travel times in the open woodland (from 4.5 min in *P. inermis* to 5.9 min in *P. mendozanus*), but very different when on roads (*P. inermis* and *P. mendozanus* decreased to 2.39 min and 2.31 min, respectively, while *P. rastratus* increased to 8.40 min; Fig. 1c).

Although the number of sampled ants per colony was similar, the mean number ( $\pm$  SD) of simultaneous foraging trails per colony differed among species ( $F_{2,21} = 31.45$ ,  $P < 0.01$ ), independent of the habitat (interaction:  $F_{2,21} = 0.19$ ,  $P = 0.83$ ; habitat:  $F_{1,21} = 0.25$ ,  $P = 0.62$ ). *Pogonomyrmex rastratus* and *P. mendozanus* showed a higher number of trails ( $5.57 \pm 0.53$  and  $4.71 \pm 0.95$ ) than *P. inermis* ( $2.43 \pm 0.53$ ) (Fig. 2, Appendices S1 - S3).

In most colonies the directions taken by foragers differed statistically from those expected under a circular random distribution for all species (Tab. 1). Measures of circular dispersion such as mean vector length, however, differed between species ( $F_{2,21} = 6.15$ ,  $P = 0.01$ ), independent of habitat (interaction:  $F_{2,21} = 0.64$ ,  $P = 0.54$ ; habitat:  $F_{1,21} = 0.7$ ,  $P = 0.42$ ). *Pogonomyrmex inermis* colonies concentrated their foraging effort in a few preferred directions compared to *P. rastratus* (higher  $r$  values), whereas *P. mendozanus* colonies showed intermediate values (not different from either of the other two species; Tab. 1 and Fig. 2). Even though *P. inermis* concentrated their foraging effort on a few trails and directions, the low frequency of foragers on each trail prevents the visual detection of foraging columns or trunk-trails in the field.

### Seed bait experiment: plasticity of foraging strategies

In general, abundant and concentrated sources of seeds placed near the nests modified the foraging behavior of the three *Pogonomyrmex* species, though in different degrees.

*Pogonomyrmex inermis* foragers detected and exploited seed bait stations two to four days after they were placed and did not modify their general foraging strategy: most foragers still traveled through two to three trails and searched for seeds in almost the same patches exploited before the experiment (Fig. 3b, Appendix S4). Accordingly, the mean vector ( $\mu$ ) of foragers was very similar before and after seed addition in six of the ten colonies sampled (Tab. 2). *Pogonomyrmex rastratus* foragers needed two to six days to discover and remove seeds from baits, and only two out of the four studied colonies showed slightly different foraging trajectories before and after seed addition (Fig. 3a, Appendix S5). Moreover, the outgoing direction of foragers near the nest entrances was very similar in both cases (Tab. 2) and several foragers continued searching for food in the same areas visited before baiting (Fig. 3a).

In contrast, *Pogonomyrmex mendozanus* modified their foraging behavior towards a group-foraging mode. Foragers discovered baits in only two to three hours; and this was soon followed by dozens of workers quickly leaving

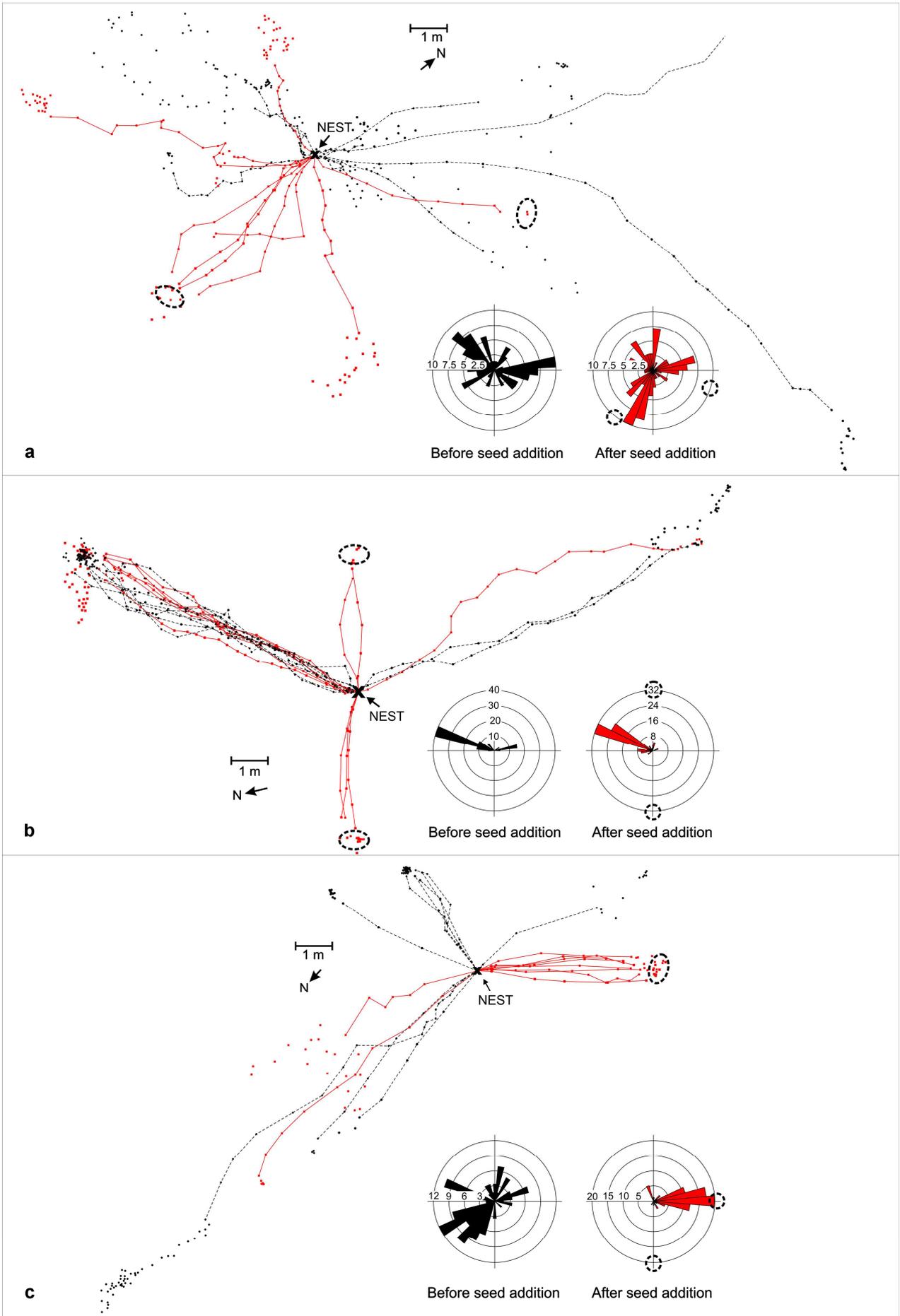
Tab. 1: Mean vector length ( $r$ ) of the outgoing directions taken by foragers of *Pogonomyrmex rastratus*, *P. inermis*, and *P. mendozanus* colonies located in the open woodland and on dirt roads in the central Monte desert. \*:  $P < 0.05$ , Rayleigh test.

	<i>P. rastratus</i>	<i>P. inermis</i>	<i>P. mendozanus</i>
Open Woodland	0.11	0.78*	0.56*
	0.34*	0.73*	0.56*
	0.57*	0.62*	0.58*
Dirt Roads	0.42*	0.42*	0.36*
	0.15	0.90*	0.28*
	0.29*	0.74*	0.54*
	0.45*	0.55*	0.39*
Overall mean $\pm$ SD	0.33 $\pm$ 0.16	0.68 $\pm$ 0.16	0.47 $\pm$ 0.12

Tab. 2: Analysis of the outgoing directions taken by foragers of *Pogonomyrmex rastratus*, *P. inermis*, and *P. mendozanus* colonies before and after experimental seed baits were offered in the central Monte desert. Mean vector ( $\mu$ ), mean vector lengths ( $r$ ), Watson's  $U^2$ , their p-values (ns:  $P > 0.05$ ; \*:  $P < 0.05$ ), the number of foragers observed by colony before/after experimental seed addition ( $N$ ), and colonies mapped on Fig. 3 ( $\rightarrow$ ) are shown.

	Before baiting		After baiting		$U^2$	P	N
	$\mu$	$r$	$\mu$	$r$			
<i>P. rastratus</i> $\rightarrow$	304°	0.15	211°	0.10	0.18	ns	75/75
	201°	0.42	105°	0.45	0.59	*	50/70
	337°	0.29	16°	0.24	0.18	ns	59/61
	91°	0.65	79°	0.51	0.15	ns	50/61
	167°	0.45	175°	0.44	0.09	ns	51/51
	42°	0.31	204°	0.44	0.74	*	51/53
<i>P. inermis</i>	231°	0.30	201°	0.82	0.75	*	70/72
	346°	0.90	16°	0.92	0.91	*	62/60
	312°	0.74	174°	0.31	0.96	*	60/60
	18°	0.55	7°	0.82	0.17	ns	52/61
	77°	0.65	90°	0.35	0.28	*	50/60
	244°	0.71	298°	0.41	1.03	*	50/62
	303°	0.63	219°	0.26	0.63	*	50/60
	198°	0.30	328°	0.35	0.58	*	62/67
	254°	0.58	161°	0.90	2.21	*	60/60
	36°	0.58	334°	0.88	1.76	*	60/65
<i>P. mendozanus</i>	138°	0.36	65°	0.73	1.60	*	73/93
	281°	0.28	196°	0.80	1.77	*	71/63
	270°	0.54	245°	0.19	0.52	*	71/72
	8°	0.39	198°	0.64	1.70	*	84/61
	6°	0.44	217°	0.75	2.46	*	64/75
	186°	0.96	358°	0.89	3.65	*	65/116
	33°	0.62	213°	0.62	2.68	*	62/116
	$\rightarrow$						

Fig. 3: Maps showing the spatial foraging patterns of workers from typical colonies of *Pogonomyrmex rastratus* (a), *P. inermis* (b), and *P. mendozanus* (c) before and after experimental seed baits were offered on dirt roads in the central Monte desert (maps of additional experimental colonies in Appendices S4 - S6). Individual travel trajectories from the next entrance (X) before (black dashed lines) and after (red solid lines) seed addition are shown. The position of seed baits are indicated by dashed circles. Circular histogram graph shows the frequencies and distribution of the outgoing directions taken by 60 foragers leaving the nest in both conditions. Map and circular graph are oriented in the same direction relative to North.



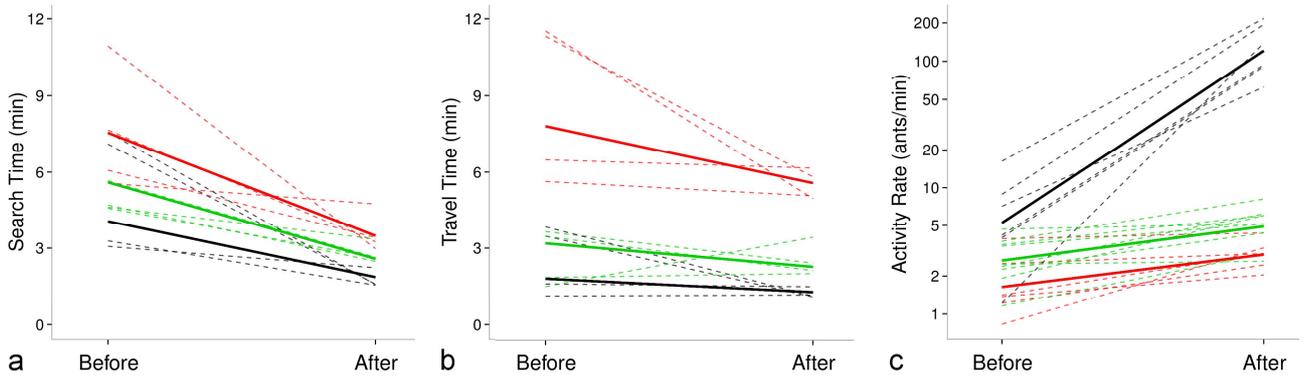


Fig. 4: Main characteristics of the individual foraging paths of *Pogonomyrmex inermis* (green), *P. mendozanus* (black), and *P. rastratus* (red) harvesting ants before and after experimental seed baits were offered on dirt roads in the central Monte desert. (a - b) Mean individual search time and mean travel time as estimated by linear mixed models (solid lines for the predicted values per species and dashed lines for each colony, estimated from eight to 13 individual foraging paths per colony in each condition). (c) Foraging activity rate of colonies (log scale) before and after seed baiting (dashed lines) and predicted values for each species (solid lines). See detailed results of linear mixed models in text.

the nest in a straight line toward the baits. Foragers spent a few seconds manipulating seeds in the baits and ran straight back to the nest carrying one seed. This behavior continued until all seeds were removed. Accordingly, the distribution of the outgoing direction of foragers recorded near nest entrances (mean vector and mean vector length) differed before and after baiting in every colony sampled (Tab. 2, Fig. 3c, Appendix S6). Although the response of *P. mendozanus* clearly involved the recruitment of many workers to seed baits, they moved as an unorganized group of ants along diffuse wide trails rather than as an aligned foraging column.

Variance among individual search times within a colony (in log-scale) were heterogeneous among species and were differentially affected by seed addition (variance estimation per Spp  $\times$  Experiment vs. homogeneous variances:  $\Delta\text{AIC} = 17.74$ ;  $L_5 = 27.74$ ,  $P < 0.001$ ). Mean intra-colony variability was high in *Pogonomyrmex rastratus* (0.348) and low in *P. inermis* (0.216) before adding seeds and both increased weakly after seed addition (18% and 16%, respectively). In contrast, mean intra-colony variability of *P. mendozanus* individual search times was similar to *P. rastratus* before seed addition (0.368) but decreased strongly after artificial seed patches were found (0.230; -38%), becoming similar to that of *P. inermis*. Both the experimental effect and the differences among species proved relevant in the final model ( $\Delta\text{AIC} = 10.28$ ;  $L_1 = 12.28$ ,  $P < 0.001$ , and  $\Delta\text{AIC} = 7.25$ ;  $L_2 = 11.25$ ,  $P = 0.004$ , respectively). The addition of seed patches, although with important variation among colonies (random Experiment  $\times$  Colony vs. random intercepts:  $\Delta\text{AIC} = 4.89$ ;  $L_5 = 8.89$ ,  $P = 0.007$ ), reduced the mean search time of the three species by a similar amount in log-scale, or a similar proportional change in units of time (Spp  $\times$  Experiment:  $\Delta\text{AIC} = -1.35$ ;  $L_5 = 2.65$ ,  $P = 0.266$ ; Fig. 4a).

For travel times (in log scale) the intra-colony variability was also affected by seed addition (different variances per Spp  $\times$  Experiment vs. homogeneous variances:  $\Delta\text{AIC} = 6.70$ ;  $L_5 = 16.70$ ,  $P = 0.004$ ), with a much stronger change in *Pogonomyrmex mendozanus* colonies (before: 0.274, after: 0.155, a 43% reduction) than in *P. inermis* (0.250 to 0.206: -17%) and *P. rastratus* (0.238 to 0.276:

+16%). The addition of seeds had a similar effect in the three species (Spp  $\times$  Experiment:  $\Delta\text{AIC} = -1.22$ ;  $L_2 = 2.78$ ,  $P = 0.249$ ), which differed in mean travel time ( $\Delta\text{AIC} = 25.97$ ;  $L_2 = 29.97$ ,  $P < 0.001$ ; Fig 4b). The global experimental effect on mean individual travel times was subtle ( $\Delta\text{AIC} = 1.00$ ;  $L_1 = 3.00$ ,  $P = 0.083$ ) maybe as a consequence of the important variation in experimental effect among colonies (random Experiment  $\times$  Colony vs. random intercepts:  $\Delta\text{AIC} = 28.11$ ;  $L_2 = 32.11$ ,  $P < 0.001$ ; Fig. 4b).

Beyond the species differences and mean global effect (fixed factors), the residual variation in magnitude of the experimental effect at the colony level was strongly inversely correlated with the previous mean search and travel times (correlation between random slopes and random intercepts: -0.925 and -0.948, respectively): reductions in mean search and travel times were stronger when foragers in the colony were taking longer to reach and search their foraging areas.

Finally, colonies of the three species responded to experimental seed addition by increasing their foraging activity rate (Fig. 4c). The increase was much more conspicuous in *Pogonomyrmex mendozanus* than in *P. inermis* and *P. rastratus* colonies (Spp  $\times$  Experiment:  $\Delta\text{AIC} = 32.12$ ;  $L_2 = 36.12$ ,  $P < 0.001$ ). On average, colonies of *P. mendozanus* increased their foraging activity 23-fold under experimental conditions (from 5.25 to 120.86 ants / min) while the other two species did not even double (*P. inermis*: 1.85 times, *P. rastratus*: 1.79 times; Fig. 4c). The variability among *Pogonomyrmex* colonies in their activity rate was much higher before (0.233) than after (0.096) seed baiting (-58%; different variances per Experiment vs. homogeneous variances:  $\Delta\text{AIC} = 2.94$ ;  $L_1 = 4.94$ ,  $P = 0.013$ ).

## Discussion

Our first objective was to describe the foraging strategy of three *Pogonomyrmex* species in two different habitats of the central Monte desert. Based on individual and group movement of ants, we have shown that *P. inermis*' workers left the nest in only two to three directions and searched for seeds on small areas that were simultaneously exploited by other nestmates. All this evidence supports group-foraging behavior, although the low frequency of

foragers on each trail prevents the visual detection of foraging columns or trunk-trails as is characteristic of congeneric North American group-foraging species (WHITFORD & al. 1976, DAVIDSON 1977, FEWELL 1988, GORDON & al. 2008). In contrast, *P. rastratus* and *P. mendozanus* displayed a solitary foraging strategy in the field. Workers radiated in almost all directions from the nest, used several travel trajectories that were not usually followed by other nestmates, and searched for and collected seeds in extensive non-overlapping areas.

Although the foraging strategy described was very similar among colonies within the open woodland and on the roads, some aspects of ant foraging behavior varied between habitats. For example, ants of colonies of *Pogonomyrmex inermis* located on dirt roads searched within a bigger area per unit time than colonies in the open woodland, and the travel time of *P. mendozanus* and *P. inermis* workers decreased on dirt roads even though they traveled farther away from the nest. In other words, foragers moved farther and faster or in a less convoluted path on roads than in the open woodland. Such differences can be attributed to habitat structural features that may affect ant movement and foraging success (CRIST & MACMAHON 1991, CRIST & WIENS 1994, FARJI-BRENER & al. 2004, OETTLER & al. 2013). Dirt roads are open areas with more bare soil and less vegetation cover than the surrounding habitats. The increase in plant cover in the open woodland may reduce forager speed (FEWELL 1988), with more physical obstacles affecting movement patterns and reducing foraging success (TORRES-CONTRERAS & VÁZQUEZ 2007). On the other hand, plant litter that accumulates beneath shrubs and trees favors the retention of seeds carried by wind and water (MARONE & al. 2004), suggesting that seeds may be more abundant in the open woodland than on roads. The combination of low seed abundance and less physical obstacles on the ground may thus explain why ants from colonies on dirt roads moved faster and searched for seeds in more extensive areas.

In many harvester ants, recruitment activity depends on the perception of trail pheromones produced and laid by foragers (HÖLLDOBLER 1976, HEREDIA & DETRAIN 2000, HÖLLDOBLER & al. 2001, PLOWES & al. 2013). Stability and intensity of pheromone trails are conditioned by the number of workers assigned to foraging, which, in turn, is related to colony size (TRANIELLO 1989, BEEKMAN & al. 2001, THOMAS & FRAMENAU 2005). Colonies of *P. inermis*, *P. rastratus* and *P. mendozanus* have 300 - 1100 workers (NOBUE-BERHMANN & al. 2010) which is much fewer than found in colonies of typical group-foraging species (TABER 1998, JOHNSON 2000). The number of foragers active outside the nest is even lower in these species than in a North American *Pogonomyrmex* displaying solitary foraging (NOBUE-BERHMANN & al. 2013). Therefore, colony size and forager abundance may significantly constrain recruitment capacity in these and other South American *Pogonomyrmex* species with small colonies (ARANDA-RICKERT & FRACCHIA 2012, BELCHIOR & al. 2012, NOBUE-BERHMANN & al. 2013).

Our second objective was to test whether the foraging strategies in these ants are flexible and change according to seed density. Field experiments showed that *Pogonomyrmex mendozanus* shifted their foraging strategy from solitary towards group-foraging after the addition of a

dense source of seeds. This response involved the recruitment of many workers that moved along diffuse trails to seed stations, as has been documented in *P. maricopa* WHEELER, 1914 and *P. californicus* (BUCKLEY, 1866) (see HÖLLDOBLER 1976, DAVIDSON 1977, CRIST & MACMAHON 1991, JOHNSON 2000, 2001). In contrast, *P. rastratus* and *P. inermis* colonies did not significantly change their foraging strategy when clumped seeds were supplied.

The addition of seed patches reduced the mean search time (and mean search area) that workers needed to find seeds. When seeds were scarce and scattered (before supplementing), colonies of *Pogonomyrmex mendozanus* and *P. rastratus* covered more ground with ants searching individually, whereas *P. inermis* foraged in groups searching in few, small foraging areas. As a consequence, intra-colony variability of search time was high and similar in *P. mendozanus* and *P. rastratus*, but low in *P. inermis*. However, when seeds were placed near the nests *P. mendozanus* colonies directed more ants to the clumped seed sources and, as a result, intra-colony variability of search time was significantly reduced. In contrast, the response of *P. rastratus* and *P. inermis* was more subtle since most foragers searched in the same patches (*P. rastratus*) or in a similar way (*P. inermis*) than before.

The reduction of search time was accompanied by an increase of colony foraging activity after seed addition. Once again, *Pogonomyrmex mendozanus* showed a much more conspicuous response than the other two species. In some harvester ants the return of foragers with food is what stimulates other foragers to leave the nest (HEREDIA & DETRAIN 2005, SCHAFER & al. 2006, GORDON & al. 2008). The more food is available, the less time is needed to search, and the more quickly a forager returns with food. Since foraging is regulated by the rate of return of successful foragers, and the duration of a foraging trip depends mostly on search time (BEVERLY & al. 2009), the reduction of search time may trigger the increase of foraging rates recorded in this study.

The shift of foraging strategy towards a group-foraging mode together with the drastic increase of foraging activity and the reduction of search time when ants were confronted with abundant and concentrated sources of seeds clearly indicate that the foraging behavior of *Pogonomyrmex mendozanus* is much more flexible than those of *P. inermis* and *P. rastratus*. Flexibility in foraging is consistent with diet breadth in this species. Previous studies have described a very narrow diet breadth of only grass seeds for *P. inermis*. In contrast, *P. mendozanus* and, to a lesser extent, *P. rastratus* became more generalist and included a higher proportion of non-grass items in their diet when grass seeds were seasonally scarce (PIRK & al. 2009, POL & al. 2011). A more generalist and flexible diet and a flexible foraging behavior may constitute important adaptive features in the central Monte desert, where seed production is irregular (POL & al. 2010, 2011) and both natural and anthropic disturbances may severely reduce the availability of preferred grass seeds (POL & al. 2014).

The way harvester ants use space for foraging determines their access and impact on seed resources (MULL & MACMAHON 1997, AZCÁRATE & PECO 2003). Workers of *Pogonomyrmex rastratus* and *P. mendozanus* search and collect seeds solitarily under natural conditions. As a result, nest surroundings are continuously and thoroughly

explored. In contrast, workers of *P. inermis* tend to move together along trails, and most of the searching takes place in a very restricted area. In consequence, foraging activity of *P. inermis* could lead to a heterogeneous distribution of seed removal and hence to the existence of small refuge microsites within ant foraging areas (DAVIDSON 1977, AZCÁRATE & PECO 2003). If seed removal rates are higher in areas of high seed density then seed removal would be a homogenizing force tending to equalize seed density across patch types in the landscape (AVGAR & al. 2008). Conversely, seed consumption by solitary foragers, as shown by *P. rastratus* and *P. mendozanus*, should result in a more uniform reduction of soil seed bank abundance within the foraging area. The spatial impact of seed removal, however, depends also on the spatial distribution and temporal persistence of foraging trails, foraging site selection, site fidelity, competition with other ants, and colony distribution (HÖLLDOBLER & WILSON 1990, CRIST & MACMAHON 1991, ACOSTA & al. 1995, CRIST & WIENS 1996, MULL & MACMAHON 1997); thus, further studies are needed to estimate the impact of these ants on the soil seed bank distribution.

Several authors have proposed that ant communities are structured by interspecific competitive interactions (HÖLLDOBLER & WILSON 1990, SANDERS & GORDON 2000, SANTINI & al. 2007, but see CERDÁ & al. 2013). Therefore, species with similar diets may coexist within local habitats only if they differ in resource utilization in time and space (DAVIDSON 1977, WHITFORD 1978, BROWN & al. 1979, HÖLLDOBLER & WILSON 1990, SOLIDA & al. 2010). In the central Monte desert, where *Pogonomyrmex rastratus*, *P. mendozanus* and *P. inermis* coexist, their diets overlap in composition, species richness and seasonal variation (PIRK & al. 2004, PIRK & LOPEZ DE CASENAVE 2006, PIRK & al. 2009) and their daily and seasonal foraging periods coincide (POL & LOPEZ DE CASENAVE 2004). Differences in the foraging strategy among species reported here may therefore represent an important factor determining their coexistence, since group and individual foragers species specialize in high-density and low-density seed resources and they make a distinctive use of space (DAVIDSON 1977).

In conclusion, based on field observations and experimental results, we determined that *Pogonomyrmex rastratus* is an exclusive solitary foraging species, while *P. inermis* use a group-foraging strategy with limited recruitment, and *P. mendozanus* display an intermediate foraging strategy in which workers are typically solitary foragers but recruit nestmates to high-density seed patches when they become available. Such differences may contribute to their coexistence and have important implications for the spatial impact of seed removal. The flexible foraging behavior shown by these harvester ants, and particularly by *P. mendozanus*, may constitute an important adaptive feature in the Monte desert where soil seed bank abundance and composition is heterogeneous, irregular and severely affected by natural and anthropic disturbances.

### Acknowledgments

We thank Gabriela Pirk for her helpful comments on an earlier version of this manuscript. Joseph Sapp helped to improve the English. Bárbara Pavan, Beatriz Nobua-Behrmann and Gabriela Pirk helped us during field work. We

acknowledge financial support granted by ANPCyT (through PICT 2196 and PICT 2010-0898) and by Universidad de Buenos Aires (UBACyT 20020100100928) from Argentina. This is contribution number 88 of the Desert Community Ecology Research Team (Ecodes) of UF&EV-IA-DIZA Institute (CONICET), and FCEN (Universidad de Buenos Aires).

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