RESEARCH ARTICLE

Forager abundance and its relationship with colony activity level in three species of South American *Pogonomyrmex* harvester ants

B. E. Nobua-Behrmann · J. Lopez de Casenave · F. A. Milesi · B. Pavan

Abstract The proportion of foragers in ant colonies is a fairly constant species-specific characteristic that could be determined by intrinsic or extrinsic factors. If intrinsic factors are relevant, species with similar life history characteristics (e.g., colony size and foraging strategies) would be expected to have a similar proportion of foragers in their colonies. Within the genus *Pogonomyrmex*, North American species can vary largely in their colony size, whereas only species with small colonies are known in South America. We studied the characteristics of the foraging subcaste in three sympatric South American species of *Pogonomyrmex* harvester ants, and compared it with the available information on other species of the same genus. We used two mark-recapture methods and colony excavations to estimate the number and proportion of foragers in the colonies of *P. mendozanus*, *P. inermis*, and *P. rastratus*, and to test the relationship between forager external activity levels and abundance per colony. Forager abundance in the three studied species was lower than in most North American species. The percentage of foragers in their colonies ranged 7–15 %, more similar to North American species with large colonies than to those with small colony size. Foraging activity was positively correlated with forager abundance in all three species, implying that colony allocation to number of foragers allows for higher food acquisition. Further comparative studies involving a wider range of traits in South and North American species would allow to unveil the role of environmental factors in shaping each species' particular traits.

Introduction

Ants are dominant members of virtually all terrestrial ecosystems (Hölldobler and Wilson, 1990). They influence these ecosystems mainly through the direct and indirect effects of their foraging via herbivory, seed dispersal, and nutrient cycling (MacKay, 1991; Mac Mahon et al., 2000; Passos and Oliveira, 2002; Verchot et al., 2003). Foraging is also a fundamental aspect of ant biology affecting colony growth, reproduction, behavior, and survival. The foraging characteristics of a colony (e.g., foraging strategies, abundance and proportion of foragers per colony, foraging activity levels) are directly related to its performance and potential impact on the ecosystem. Ant colonies tend to grow logistically to some approximately constant size (Hölldobler and Wilson, 1990). The number of foragers in those colonies also tends to increase rapidly after colony founding and reach relatively stable levels in few years and for the entire active life of the colony (Gordon, 1992, 1995; Gordon and Kulig, 1996). The proportion of foragers in the colony is, then, a relatively constant feature characteristic of each ant species. This character could be related to intrinsic factors (e.g., worker replacement rates, colony's energy budget, worker's physiology) or to extrinsic factors (e.g., variations in resource abundance, resource quality, environmental conditions, competition). Comparative studies keeping one group of factors (relatively) constant would

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allow to assess the importance of the other group to explain the variation of this life history character.

The genus *Pogonomyrmex* comprises 74 species of harvester ants that inhabit the arid and semiarid habitats of the New World. They are segregated in two distinct distribution areas with no shared species between them: most of South America and southwestern North America (Kusnezov, 1951; Taber, 1998). North American species can vary largely in their colony size (100–10,000 workers; Johnson, 2000), while all known South American species are rather small (<2,000 workers; Kusnezov, 1951; Nobua Behrmann et al., 2010). Most studies have focused on the North American species, particularly on those species with large colonies (>2,000–10,000 workers), group foraging strategies, and 200–2,000 foragers per colony (MacKay, 1981; Gordon, 1992; Tschinkel, 1998, 1999; Smith and Tschinkel, 2006). Specific studies on *P. rugosus*, *P. subnitidus*, *P. badius*, and *P. salinus* showed that foragers represent 9–19 % of total colony size (Golley and Gentry, 1964; Porter and Jorgensen, 1980; MacKay, 1981). In North American species with small colony size and solitary foraging strategies, though scarcely studied, it seems that the number of workers devoted to foraging is smaller (200–900 foragers per colony) but represents a higher proportion of total colony (Whitford and Ettershank, 1975; MacKay, 1981). Direct measures of the percentage of foragers in individual colonies support that pattern: up to 23 % in *P. montanus* (MacKay, 1981). The tentative general pattern for North American species is that those with small colony size and solitary foraging strategies allocate a higher proportion of their working force into foraging than those species with larger colonies and group foraging strategy.

The colony size and composition of the South American *Pogonomyrmex* species have not been studied in detail so far. The little information available shows that they usually have small colonies, with individual foraging or limited recruitment (Kusnezov, 1951; Pol, 2008; Nobua Behrmann et al., 2010). To date, there is no detailed information on the number and proportion of foragers in South American species or how they relate to foraging activity, which may provide valuable information for comparative studies within a closely related group of ants depending on a rather specific resource (i.e., seeds). If colony task organization and energetic sustainability (i.e., intrinsic factors) put a strong and similar lower limit on the number of workers required to sustain a colony foraging for seeds, we would expect the proportion of foragers in their colonies to be similar to those in North American species with small colonies and individual foraging strategies. Otherwise, variable proportions of foragers among species or a similar proportion to those of North American species with large colonies would suggest that environmental or ecological factors (i.e., extrinsic

factors) are stronger determinants of energy allocation to resource acquisition.

We studied the characteristics of the foraging caste in three sympatric species inhabiting the central Monte desert of Argentina: *Pogonomyrmex mendozanus*, *P. inermis*, and *P. rastratus*. We used two mark-recapture methods and colony excavations to estimate the number and proportion of foragers in their colonies. We also studied the relationship between forager abundance per colony and external activity levels in these three species to sustain the logical assumption that colony allocation of number of workers to foraging tasks implies a potentially higher foraging effort. Previous studies showed that daily changes in foraging activity levels are coarsely driven by temperature (Pol and Lopez de Casenave, 2004), although temperature by itself failed to explain the high variability in foraging activity observed among colonies. We expect that when temperature is within its optimal range, foraging activity will be positively correlated to the abundance of foragers in a colony.

Materials and methods

Study area and species

The study was carried out at the Biosphere Reserve of Ñacuñán (34°03′S, 67°54′W, Mendoza Province, Argentina), in the central portion of the Monte desert. The climate in Ñacuñán is dry and temperate with marked seasonality. Mean annual temperature is 15.6 °C (Lopez de Casenave, 2001), and mean annual rainfall is 343.6 mm (1972–2005) with high year-to-year variation. Most rainfall occurs in spring and summer (October–March). The main habitat is an open woodland of *Prosopis flexuosa*, where trees are scattered within a matrix of perennial tall shrubs (mostly *Larrea divaricata*), low shrubs, perennial grasses, and bare ground. Annual forb cover is highly variable from year to year, though it is usually much lower than grass cover.

Pogonomyrmex mendozanus, *P. inermis*, and *P. rastratus* are three species of harvester ants that inhabit the central Monte desert. It should be noted that the taxonomic status of *P. mendozanus* has been only recently established (Cuezzo and Claver, 2009). We studied the same population but it was considered *P. pronotalis* (following Claver and Fowler, 1993) in previous studies (e.g., Pol and Lopez de Casenave, 2004; Pirk and Lopez de Casenave, 2006; Pirk et al., 2009). All of them are specialized granivores with a strong preference for grass seeds (Pirk and Lopez de Casenave, 2006, 2010; Pirk et al., 2009) and they have relatively small colonies (300–1,100 workers; Nobua Behrmann et al., 2010) with low activity levels (Pol and Lopez de Casenave, 2004).

Forager abundance

During February 2007, we estimated the abundance of foragers in five colonies of each species using capture-mark-recapture techniques. Capturing and recapturing were conducted in the morning and afternoon when external activity level was highest (Pol and Lopez de Casenave, 2004). Foragers were defined as any ant that crossed a 35 cm diameter circle around the nest entrance. We captured all foragers at each nest entrance until a 10-min period without external activity or for a maximum of 1 h. Captured ants were temporarily kept in plastic containers, counted, marked, and immediately released near the nest entrance. Ants were marked by drawing a dot on their gaster with an oil-based paint marker (Uni Paint, Mitsubishi Pencil Co.). We previously corroborated in laboratory assays that the marking process and the mark itself did not affect these ants' survival, behavior and nestmate recognition (detailed results in Nobua Behrmann, 2008). We performed 7–11 subsequent capture events (recaptures) in each colony, each of them separated by 24–48 h.

We estimated the abundance of foragers in each colony using two mark-recapture data analysis methods: the Petersen method and the Schnabel method (Seber, 1982; Krebs, 1999). Both methods share the same basic assumptions: (1) the population is closed, (2) every individual has the same chance of being caught, (3) marks are not lost or transferred, and (4) marks do not affect individuals' life expectancy.

The Petersen index (also known as Lincoln index; Seber, 1982) only considers two capture events and estimates forager abundance (N_{Pet}) as:

$$N_{Pet} = [(n_1 + 1)(n_2 + 1)/(m_2 + 1)] - 1, \quad (1)$$

where n_1 and n_2 are the total number of individuals captured in the first and second sampling, respectively, and m_2 is the number of marked individuals captured in the second sampling. The Schnabel method is an extension of Petersen method intended for several successive sampling events. In this case, forager abundance (N_{Sch}) is estimated as:

$$N_{Sch} = \Sigma(n_i M_i)/\Sigma m_i, \quad (2)$$

where n_i is the total number of individuals captured in sample i, m_i is the number of marked individuals captured in sample i, and M_i is the number of marked individuals in the population before sample i was taken. For each estimate we calculated 95 % confidence intervals following Seber (1982). We compared forager abundance among the three species with a one-way ANOVA.

Colony excavations

We excavated two of the five studied colonies per species 1–6 days after the last recapture (i.e., 10–17 days after the first capture) in order to assess the total number of ants per colony and calculate the percentage of foragers. The excavations started at dawn, when soil temperature is low and these species have no external activity (Pol and Lopez de Casenave, 2004) so all the workers from the colony were inside the nest. We removed a thin layer of soil in order to delimit the area around the nest entrance with chambers and tunnels, and continued systematically removing 2-cm soil layers capturing every individual we found. Removed soil was sieved to guarantee that all ants were captured. In all cases, we continued excavating 20–50 cm deeper after the last ant, chamber or tunnel was detected, in order to ensure we recovered the entire colony.

We found brood in five of the six excavated nests (exception was nest I7 from *P. inermis*) and captured the colony queen in half of the nests. Since *Pogonomyrmex* species typically present top-heavy nests (MacKay, 1981; Tschinkel, 2003, 2004), and in all cases we continued excavating for up to 50 cm deeper after the last ant, chamber or tunnel was detected, we assume that we captured all the ants in the colony. Maximum depth of the excavated nests ranged 92–150 cm. We counted the number of marked and unmarked workers found in each colony.

Forager abundance and external activity

We measured the external activity level of each colony on either four or five different days. Activity measurements were always performed a few minutes before starting the mark-recapture sampling on each colony. To measure activity level, we counted the number of foragers entering or leaving the nest for 3 min for *P. inermis* and *P. mendozanus*, and 6 min for *P. rastratus* during their activity peaks (late morning and afternoon during summer; see Pol and Lopez de Casenave, 2004). We confirmed that activity levels were recorded within the soil surface temperature range of maximum activity for each species (30–45 °C; Pol and Lopez de Casenave, 2004) by measuring it near the nest entrance. We fit data to an ANCOVA-like linear multiple regression model with activity level as the dependent variable, number of foragers (estimated with the Petersen method) as a continuous predictor variable, and species as a categorical predictor variable. We tested the interaction among species and number of foragers in order to test for homogeneity of slopes among species. All statistical analyses were performed using the software InfoStat (2009).

Results

Estimates of forager abundance with the Schnabel method were always higher than those following the Petersen method, although their precision was similar (Table 1).

Table 1 Forager abundance in colonies of *Pogonomyrmex mendozanus*, *P. inermis* and *P. rastratus* in the central Monte desert, as estimated by Petersen (N_{Pet}) and Schnabel (N_{Sch}) methods, with their 95 % confidence intervals in parentheses. The last column (*n*) shows the number of successive sampling events used for Schnabel's estimates. Average forager abundance ($\pm$ SD) is shown for each species. Data from nest I7 of *P. inermis* was excluded from the analysis (see text for further information)

Colony	N_{Pet} (CI 95 %)	N_{Sch} (CI 95 %)	n
P. mendozanus			
M2	90 (79–100)	203 (186–222)	10
M3	52 (45–60)	109 (97–124)	10
M4	242 (237–247)	361 (337–388)	10
M5	89 (82–96)	155 (140–173)	10
M6	68 (59–77)	103 (92–117)	10
Average $\pm$ SD	108 $\pm$ 76	186 $\pm$ 106	
P. inermis			
I5	56 (39–73)	88 (74–109)	11
I7	96 (83–109)	125 (110–144)	10
I8	71 (60–81)	104 (91–122)	10
I9	44 (20–68)	54 (46–64)	10
I10	15 (11–18)	35 (29–44)	10
Average $\pm$ SD	47 $\pm$ 24	70 $\pm$ 31	
P. rastratus			
R4	96 (81–112)	124 (108–146)	10
R5	78 (54–102)	133 (119–151)	10
R6	128 (117–140)	156 (140–175)	8
R7	42 (34–49)	63 (51–84)	9
R8	39 (33–45)	51 (42–65)	7
Average $\pm$ SD	77 $\pm$ 38	105 $\pm$ 46	

Species did not differ in the mean abundance of foragers per colony (Petersen: $F_{2,12} = 1.25$, $p = 0.32$; Schnabel: $F_{2,12} = 3.1$, $p = 0.08$). Forager abundance was highly variable among colonies of the same species (Table 1).

During excavations, we captured 219–1,077 workers per colony (Table 2). Marked ants (i.e., foragers marked during previous days) were found only in the upper chambers close to the soil surface. Number of marked workers found in the nest during excavation was always much lower than the total number of ants marked during the mark-recapture sampling period: around 40 % (Table 2). According to our estimates of forager abundance by the Petersen method,

foragers represented 7–15 % of total number of workers in the colony (Table 2). Only one of the colonies did not fit this general pattern: in the *P. inermis* colony I7, the estimated proportion of foragers was three times higher (44 %, Table 2), substantially fewer marked ants were recovered (13 %), and it was the only excavated nest where no larvae or pupae were found. This probably indicates that I7 was either a senescent colony or a colony fragment. Coincidentally, workers of *P. inermis* were occasionally observed using several adjacent nests in the study area (Lopez de Casenave and Milesi, pers. obs.). Consequently, we decided to exclude data from nest I7 from our following analyses.

Table 2 Number of marked and unmarked workers found in excavated colonies of *Pogonomyrmex mendozanus*, *P. inermis* and *P. rastratus* in the central Monte desert. For each colony, the total number of foragers marked during mark-recapture sampling (total marked ants), the percentage of those marked ants recovered during excavation, forager abundance estimated by Petersen method, and the estimated percentage of foragers are shown

	P. mendozanus		*P. inermis*		*P. rastratus*	
	M2	M3	I5	I7	R4	R5
Excavated workers	691	538	378	219	916	1,077
Marked	94	42	28	18	49	60
Unmarked	597	496	350	201	867	1,017
Total marked ants	230	127	78	142	123	150
Percentage of marked ants recovered	41	38	36	13	40	40
Forager abundance (N_{Pet})	90	52	56	96	96	78
Percentage of foragers	13	10	15	44	10	7

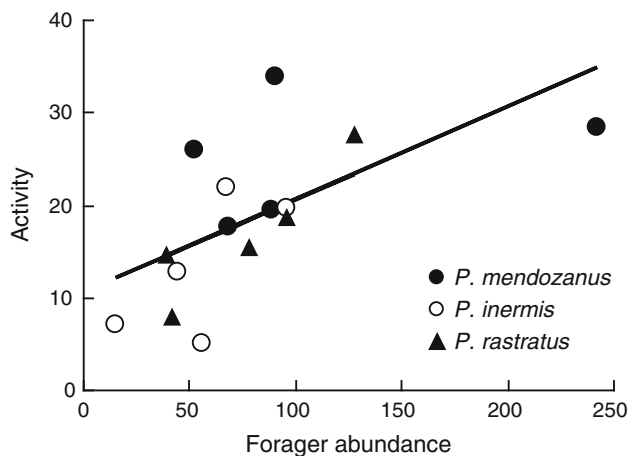**Fig. 1** Mean activity level as a function of forager abundance in colonies of *P. mendozanus* (*full circles*), *P. inermis* (*empty circles*), and *P. rastratus* (*triangles*). No significant differences were found among species. *Line* represents the simplest significant (*p* = 0.011) linear regression model, resulting from pooling data from the three species

We found a positive linear relationship between external activity level and estimated number of foragers in the colony (Fig. 1). We found no difference in mean activity level among species (Contrast 1 [*P. mendozanus* vs. *P. inermis*]: $F_{1,11}$ = 2.07, *p* = 0.18; Contrast 2 [*P. rastratus* vs. *P. inermis*]: $F_{1,11}$ = 0.27, *p* = 0.61) or the slope of the regression (Difference of slopes 1 [*P. mendozanus* vs. *P. inermis*]: $F_{1,9}$ = 2.38, *p* = 0.13; Difference of slopes 2 [*P. rastratus* vs. *P. inermis*]: $F_{1,9}$ = 0.0002, *p* = 0.99). The simplest linear regression model (pooling the data from the three species) was: activity = $10.64 + 0.1 \, N_{\text{foragers}}$ ($F_{1,13}$ = 8.02; *p* = 0.01), although it explained only a third of total variation (R^2 = 0.35).

Discussion

Mark-recapture techniques proved useful to estimate forager abundance, though estimates using the Schnabel method were always higher than those following the Petersen method (i.e., for every colony of every species). Since no mark loss was recorded during previous lab experiments in these species (Nobua Behrmann, 2008), the most likely explanation for this difference is a violation of the closed population assumption, probably due to foragers loss (mortality) during the sampling period. In concordance, the number of marked ants recovered after nest excavations was considerably lower than the total number of foragers marked during the previous days (around 40 %). Average forager lifespan in other species of this genus proved rather short: 14 days for *P. salinus* (Porter and Jorgensen, 1981) and 30–35 days for *P. barbatus* and *P. rugosus* (Gordon and

Hölldobler, 1987; Oettler and Johnson, 2009). Our results suggest that foragers of *P. inermis*, *P. mendozanus*, and *P. rastratus* may also have a relatively short average lifespan, in the order of a few weeks. Petersen method allows for a lower influence of time-dependent loss of foragers, since it can be calculated with only two consecutive sampling events (i.e., 2 days according to our protocol). In consequence, we base further analyses on these short-time estimates which probably reflect more accurately the number of foragers at a given point in time.

The average forager abundances in *P. mendozanus*, *P. inermis*, and *P. rastratus* were rather low, even lower than in those North American *Pogonomyrmex* species with small colony size. However, the proportion of foragers per colony was similar among species and more similar to the North American species with large colonies and group foraging strategy than to the ones with small colonies and individual foraging strategy (Golley and Gentry, 1964; Porter and Jorgensen, 1980; MacKay, 1981). These South American species appear to consistently allocate a smaller fraction of their colony into foraging than their North American equivalents. Since they are all strongly related species (all belonging to the same genus), it seems unlikely that those differences could be explained by intrinsic, evolutionary constrained factors such as colony physiology and energy budget. In contrast, this deviation from the general pattern found in North America suggests that South American species are subject to different environmental or ecological pressures (e.g., seed availability, spatial distribution of seeds, competition) that strongly influence the foraging allocation in their colonies. Total grass seeds production is similar in North and South American warm deserts (Marone and Horno, 1997). However, the absence of *Pogonomyrmex* species with big colonies in South America may represent a comparative advantage for the small-colony native species. Without the strong competitive effect of other species with the same requirements but substantially bigger colonies, the actual seed availability for South American *Pogonomyrmex* species may be higher than the one experienced by their North American counterparts with small colonies. In such a relatively seed-enriched environment, South American foragers would spend less time searching for seeds, thus increasing their foraging efficiency, and therefore their colonies may allocate a smaller proportion of workers to foraging activities in order to sustain the whole colony.

For the three studied species, each colony's foraging effort proved to be directly related to the number of workers allocated to foraging tasks. Previous studies on *P. mendozanus* and *P. rastratus* colonies reported surface soil temperature as one of the main factors affecting daily and seasonal activity levels (Pol and Lopez de Casenave, 2004), and that conclusion can easily be extended to *P. inermis* which have similar daily cycles (pers. obs.). However, in reporting a high variability in

activity levels among colonies, Pol and Lopez de Casenave (2004) did not analyze the influence of colony size or forager abundance. We found that when soil temperature is not such a relevant factor (i.e., within the optimal range), colonies with more foragers have higher activity levels in the three studied species. However, there was still a considerable amount of variation in activity levels that could neither be explained by forager abundance. Other factors that may influence activity patterns are predation (Gentry, 1974), competitive interactions (De Vita, 1979; Gordon 1984) or variable food availability (Crist and MacMahon, 1991; Gordon, 1991; Schafer et al., 2006; Beverly et al., 2009; Pol et al., 2011).

In conclusion, this study provides information about colony size, number and proportion of foragers and their relation with foraging activity levels on three sympatric South American species of the genus *Pogonomyrmex*. Despite their colony sizes differing by an order of magnitude, the allocation of workers to the foraging task in these South American species looks similar to what was found in North American species with large colonies. The absence of *Pogonomyrmex* species with big colonies in South American deserts could be a factor contributing to the observed pattern. More studies on the foraging characteristics of South and North American species (particularly those with small colony size) and their relation with seed availability are needed in order to assess the role of the environment in shaping the particular traits of each species.

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