Fasting and chemical signals affect recruitment and foraging efficiency in the harvester ant, *Pogonomyrmex vermiculatus*

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Summary

Ants are central-place foragers, their foraging strategies varying from solitary to group foraging. Although the ancestral South American species, *Pogonomyrmex vermiculatus*, produces alkylpyrazines which attract foragers, this species exhibits solitary foraging behaviour in the field. This restriction was explored by evaluating the effects of fasting and presence of artificially applied trail pheromones on recruitment and foraging of *P. vermiculatus*. A circular arena connected to the nest at its center was divided into 12 equal sectors with a screen near the peripheral end of each sector. Prey was offered behind the screen in one of the sectors to ants exposed to different periods of fasting. A pyrazines trail was applied or not to the sector with prey. In general, the number of active foragers in the experimental arena depended on experimentation time. Preferential and time-dependent recruitment was observed in the sector with pyrazines. The colonies that used the pyrazines trail discovered the food patch faster and removed prey at a higher rate than colonies not exposed to pyrazines. Collectively, the results show that in *Pogonomyrmex* species, the ancestral character 'solitary foraging' shows behavioural plasticity when ants are confronted with trail pheromones stimuli and are under fasting stress.

Keywords: solitary foraging, colony size, pyrazines trail.

Introduction

Ants are central-place foragers (Orians & Pearson, 1979; Stephens & Krebs, 1986), that is, forager workers search for, collect, and transport food along

radii converging at the nest entrance (Harkness & Maroudas, 1985; Bailey & Polis, 1987). The foraging strategies in these social insects can vary between solitary and group foraging (Oster & Wilson, 1978; Hölldobler & Wilson, 1990). In solitary-foraging ants, workers in motion use mainly visual perception to recognise landmarks in the landscape and/or signs in the sky (e.g., Collet et al., 1998; Schatz et al., 1999). In group-foraging ants, the recruitment of workers is determined essentially by the production and perception of trail pheromones (Hölldobler, 1984; Morgan, 1984; Traniello & Robson, 1995).

Harvester ants collect and store seeds for later consumption. They are particularly frequent and abundant in arid and semiarid zones (Hölldobler & Wilson, 1990; MacMahon et al., 2000; Johnson, 2001). *Pogonomyrmex* (subfamily Myrmicinae) is one of the main genera of harvester ants (Hölldobler & Wilson, 1990) and consists of approximately 60 species (MacMahon et al., 2000; Johnson, 2001). This genus originated approximately 60 million years ago in the north-western region of South America, and went through an adaptive radiation towards south-western North America and the north of Argentina and Chile (Kusnezov, 1963; Taber, 1998). At present, the genus is distributed from southern Canada to Tierra del Fuego (Gallardo, 1932; Kusnezov, 1951, 1963; Taber, 1998; MacMahon et al., 2000).

The genus *Pogonomyrmex* comprises species with a wide diversity of foraging behaviours. While the North American species can exhibit group foraging, the South American species are exclusively solitary foragers (Johnson, 2001). In *Pogonomyrmex*, group foraging behaviour with recruitment of individuals is determined mainly by trail pheromones secreted from the poison and Dufour glands (Taber, 1998; Hölldobler et al., 2001), although directional fidelity to trunk routes after massive disturbances such as rainfalls may depend on visual orientation based on the sun compass and familiar landmarks (Hölldobler, 1976; Bregy et al., 2008). The major compounds produced by the poison gland are alkylpyrazines (Hölldobler et al., 2001; Torres-Contreras et al., 2007), which function as short-lived signals (20–30 min) allowing the recruitment of individuals and their long-distance search for food patches (Hölldobler et al., 2001). The Dufour gland contains many fatty acid derivatives and terpenes (Hölldobler et al., 2004; Torres-Contreras et al., 2007), which serve as long-lasting orientation signals (of the order of hours) allowing the continuous reinforcement of the trail leading to the foraging site (Hölldobler et al., 2004 and references therein).

Fasting level is an important stimulus affecting the collective foraging behaviour in ants (Traniello, 1977; Cosens & Toussaint, 1986). For example, fasting can increase the consumption rates of workers (Bass, 1997) and trigger in foragers the laying of recruitment trails when resources are unlimited (Mailleux et al., 2006). We have demonstrated that the South American species, *Pogonomyrmex vermiculatus* Emery, 1905, can produce and perceive alkylpyrazines (Torres-Contreras et al., 2007), in spite of which it exhibits solitary-foraging in nature. We now inquire whether physiological state and artificial chemical trails may affect the recruitment of individuals and group foraging behaviour in this species.

Methods

Study species and experimental arena

Recruitment and foraging behaviours were studied in *P. vermiculatus*, an ant species particularly common in semiarid habitats of Chile (Snelling & Hunt, 1975). These ants construct their nests in open spaces or at the base of shrubs. The entrance of the nest has characteristic hillocks of seed remains, which are deposited by the ants after processing the fruits brought into the nest. The seeds of annual plants form a prominent part of their diet (Snelling & Hunt, 1975). The daily activity of ants begins at dawn with a period of nest cleaning, followed by a period of exploratory and foraging activities. The foraging range of *P. vermiculatus* colonies commonly extends up to 10 m from the nest entrance, and the number of foraging workers in 10 colonies observed — which contained between 170 and 560 individuals — varied between 23 and 69, mean = 46.7, SE = 5.18 (Torres-Contreras, unpublished data). These activities are performed until the soil temperature reaches about 50°C. When this temperature threshold is attained, the entrance of the nest is closed with vegetable material or small stones, and activities above ground cease.

During the Austral summer of 2006, ten nests of *P. vermiculatus* were identified in Las Chinchillas National Reserve (31°30′S, 71°06′W), a semi-desert area of Chile located 300 km north of Santiago. Colonies were carefully extracted and as many workers as possible were removed. The number of workers removed per colony ranged from 204 to 548 individuals (349.90 ± 38.39, mean ± SE). In the field, colonies were transferred to 50 × 20 × 10 cm (length × width × height) plastic boxes (artificial nests) containing four 1.5 × 16 cm (diameter × length) glass tubes with wet cotton

inside. In the laboratory, ants were acclimated during one week in the artificial nests maintained at 25°C with a 12:12 h light/dark photoperiod cycle. For experiments, each nest was connected to the centre of a 180 cm diameter circular arena by means of a 1×20 cm (diameter $\times$ length) vinyl tube. The floor of the arena was made of white melamine-coated wood lined with filter paper. Twelve equal sectors were marked on the filter paper with a pencil. The wall of the arena consisted of 10×0.5 cm (height $\times$ thickness) translucent Plexiglas which was coated on the inside with Fluon to prevent the ants from escaping.

Experimental design

Commercially available compacted sugar microspheres (5.61 ± 0.05 mg, mean $\pm$ SE, $N = 100$) were used as prey items. Field experiments revealed that ants removed this food item (Torres-Contreras, unpublished data). In the arena, a food patch consisting of 200 prey items was located at a distance of 80 cm from the nest entrance in a randomly chosen sector. In order to eliminate the possibility that workers used visual signals in their orientation towards the food patch, the preys was placed behind a small cardboard screen. Similar screens were placed in the remaining 11 sectors.

We first evaluated whether workers were able to deposit trail pheromones on the filter paper that covered the experimental arena after 7 days of fasting. After 2 h, the sector of filter paper where the greatest activity of ants was observed was cut and immersed in 100 ml of diethyl ether during 5 min. Subsequently, the solution was filtered and concentrated to approx. 50 μl. Aliquots of 1 μl were injected into an HP-5890 gas chromatograph coupled to an HP-5972 mass selective detector with an integrated data system (GC-MS analysis). Following a standard methodology (see, for example, Torres-Contreras et al., 2007), the presence of compounds in the chromatographic profile of solution was determined by comparison of mass spectra with a library database.

Artificial nests were maintained under a closed economy of feeding, that is, workers could obtain food only during the experimental trials (e.g., McNamara & Houston, 1989). Before the experiments, ants had no previous contact with the artificial prey items offered during the trials. The food patch was progressively depleted throughout each experiment. Colonies were assigned to two groups of five, which did not differ in colony size

($Z = 0.18$, $p = 0.85$). One group was tested on clean arenas and the other on arenas containing a mixture of 2,5-dimethylpyrazine (Aldrich), 2,3,5-trimethylpyrazine (Aldrich), and 3-ethyl-2,5-dimethylpyrazine (Carlos Cramer Productos Aromáticos) in the proportions found in the poison gland (Torres-Contreras et al., 2007). The effect of a pyrazines trail on foraging behaviour was assessed by spreading 50 μl of the pyrazines mixture (two-gland equivalents) on a randomly chosen sector of the arena. A similar concentration of pyrazine trail in a Y-olfactometer was able to recruit foragers (Torres-Contreras et al., 2007). The trail extended from the nest entrance to the food patch. The effect of physiological state was assessed by performing experiments after 7, 21 or 49 days of fasting.

The recruitment and foraging behaviours of forager workers were recorded with a video camera (Sony CCD-TRV 108) fitted with a 0.6 × conversion lens (Sony VCL-0637H) and located 150 cm above the centre of the arena. Only one experiment with any given colony was performed per day. Experiments began at 1000 h by connecting a colony box to the arena. When the first ant entered the arena, video recording started, and the behaviour of the colony was recorded during 120 min. After each experiment, the filter paper liner was replaced and the arena was cleaned with ethanol to eliminate potential chemical marks left by the workers. Videos were played back and the following dependent variables determined: number of active foragers present in the experimental arena and particularly in the sector containing the prey items, number of foragers recruited in the sector with pyrazines trail, time to discovery of food patch (first ant to touch a prey item), and number of preys captured per colony (a removal event was considered successful when a prey was introduced to the nest by a forager).

Statistical analyses

The data on number of active foragers and the proportion of foragers recruited in the food patch sector were analysed using repeated-measures ANOVAs. Simple linear regressions were used to analyse the relationships between colony size and proportion of foragers, and between colony size and time to discover the food patch. The effects of pyrazines trails and fasting period on time to discover the food patch and on number of captured prey items were analysed with a two-way ANOVA, using the colony as covariate. All tests were carried out with the Statistica 6.0 software (StatSoft). Data shown in figures correspond to the mean of the colonies. Data satisfied the assumptions of each test.

Results

After 7 days of fasting, the forager ants brought from the field that had access to a novel arena and offered an abundant food patch did not deposit pyrazines.

After 7, 21 and 49 days of fasting, the number of active foragers in the experimental arena without pyrazines increased and after ca. 50 min reached a plateau. The number of foragers in the arena depended significantly on the experimentation time ($F = 1.72$, df $= 24$, $p < 0.05$; $F = 14.54$, df $= 24$, $p \ll 0.001$; $F = 7.94$, df $= 24$, $p \ll 0.001$, for 7, 21 and 49 days of fasting, respectively; Figure 1A). In the experimental arena with pyrazines, after 7 and 21 days of fasting the number of active foragers in the experimental arena increased continuously. The number of active foragers depended significantly on experimentation time for 7 and 21 days of fasting ($F = 15.84$, df $= 24$, $p < 0.001$; $F = 10.72$, df $= 24$, $p \ll 0.0001$, respectively; Figure 1B) but not for 49 days of fasting ($F = 1.40$, df $= 24$, $p = 0.13$; Figure 1B). The number of workers at the end of the experiments was around 25–35 individuals under all circumstances.

In the experimental arena without pyrazines, the proportion of foragers in the sector with the food patch did not depend significantly on experimentation time after 7 and 21 days of fasting ($F = 0.81$, df $= 19$, $p = 0.69$; $F = 0.95$, df $= 19$, $p = 0.52$, respectively; Figure 1C), but did depend after 49 days of fasting ($F = 1.93$, df $= 19$, $p < 0.05$; Figure 1C). The sector with food patch was used with an occurrence lower or similar to the random probability of use, that is, 1/12 (0.083). In the presence of the pyrazines, the proportion of foragers recruited by the trail leading to the food patch depended significantly on experimentation time after 21 and 49 days of fasting ($F = 1.82$, df $= 19$, $p < 0.05$; $F = 3.29$, df $= 19$, $p < 0.001$, respectively, Figure 1D), but not after 7 days of fasting ($F = 1.14$, df $= 19$, $p = 0.32$; Figure 1D). The sector with pyrazines was used — under the three conditions of fasting — with an occurrence higher than the random probability of use.

In the experimental arena without pyrazines, no significant relationship was found between colony size and proportion of foragers ($r^2 = 0.12$, $t = 0.65$, $p = 0.56$) nor between colony size and time to discover the food patch ($r^2 = 0.01$, $t = 0.17$, $p = 0.87$). However, in the experimental arena with pyrazines a negative and marginally significant relationship was found between colony size and percentage of active foragers ($r^2 = 0.76$, $t = 3.05$,
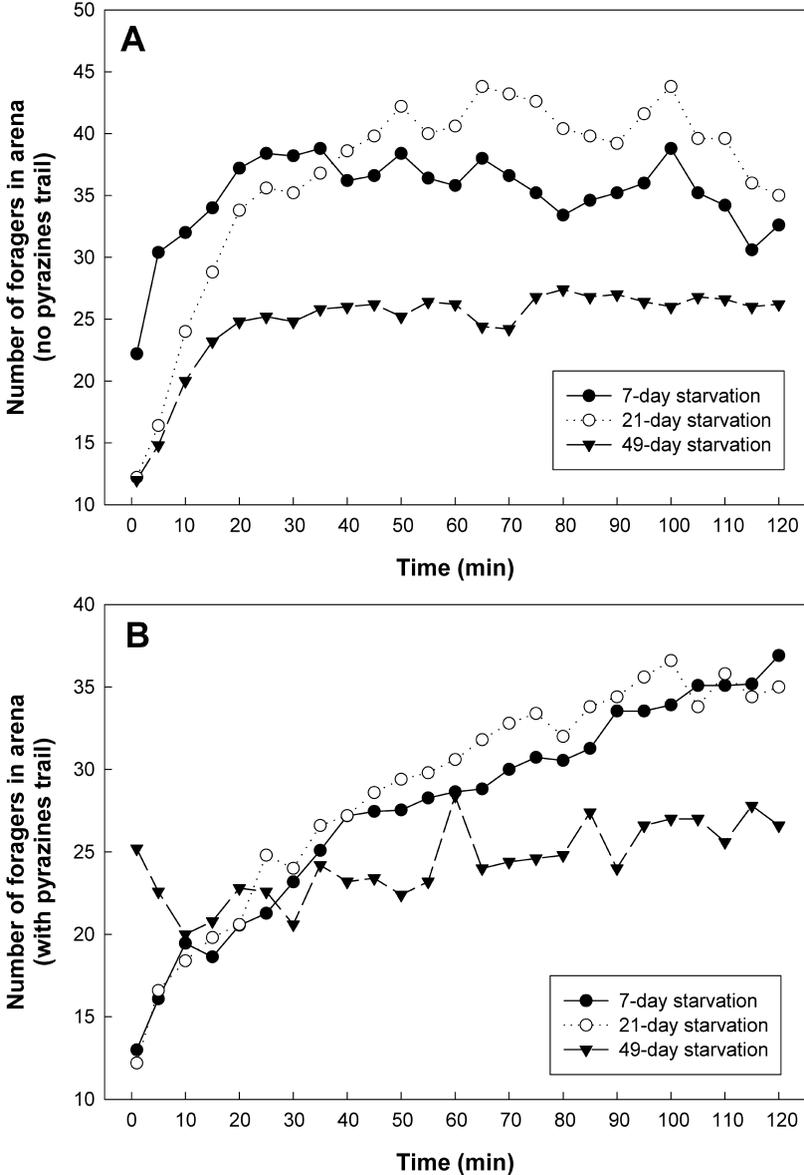
Figure 1. Effect of exploration times on the number of active foragers of *Pogonomyrmex vermiculatus* outside the nest without and with pyrazines stimuli (A and B, respectively), and the proportion of foragers recruited without and with the pyrazine trail (C and D, respectively) after fasting periods of different duration. Values are means of 5 colonies. The hatched line in plate C and D represents the random probability of being found in any given sector $(1/12 = 0.083)$. The first observations were made 1 min after the first ant entered the arena.
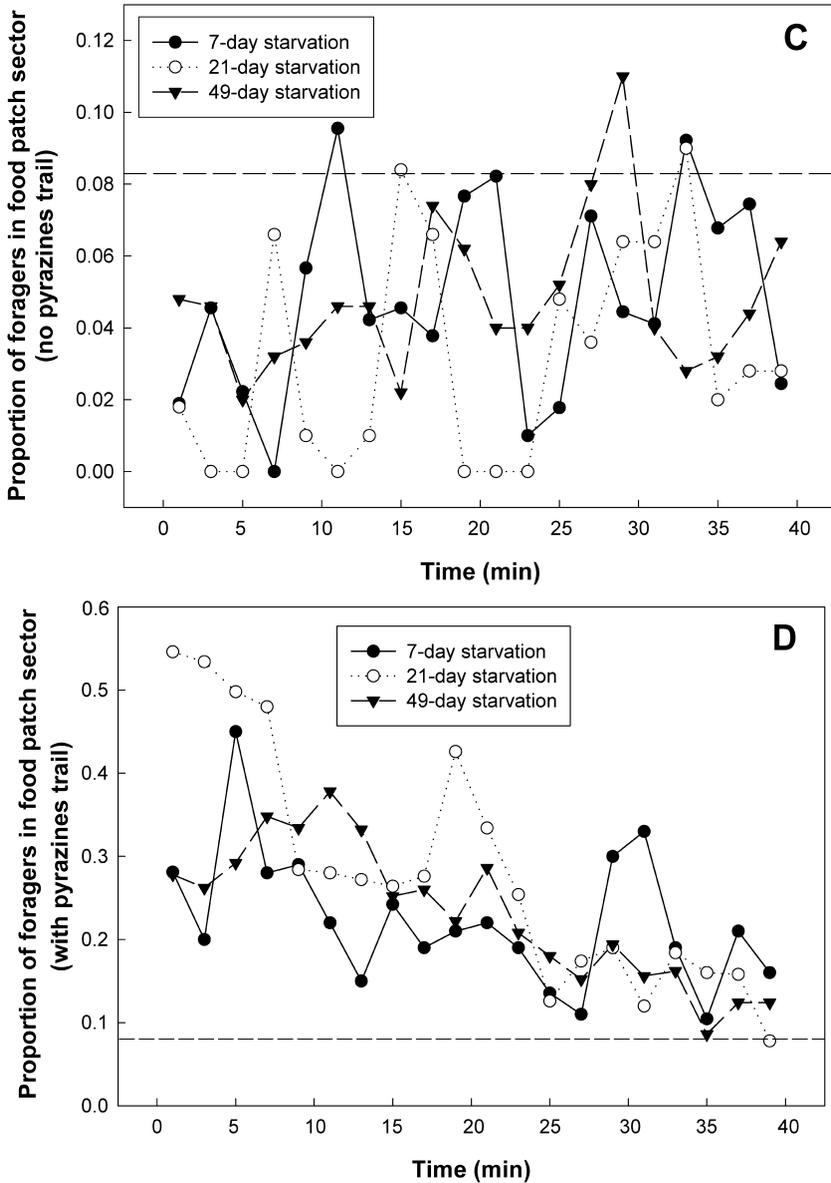
Figure 1.   (Continued.)

$p = 0.055$; Figure 2A), and a negative and significant relationship was found between colony size and time to discover the food patch ($r^2 = 0.86$, $t = 4.22$, $p < 0.05$; Figure 2B).
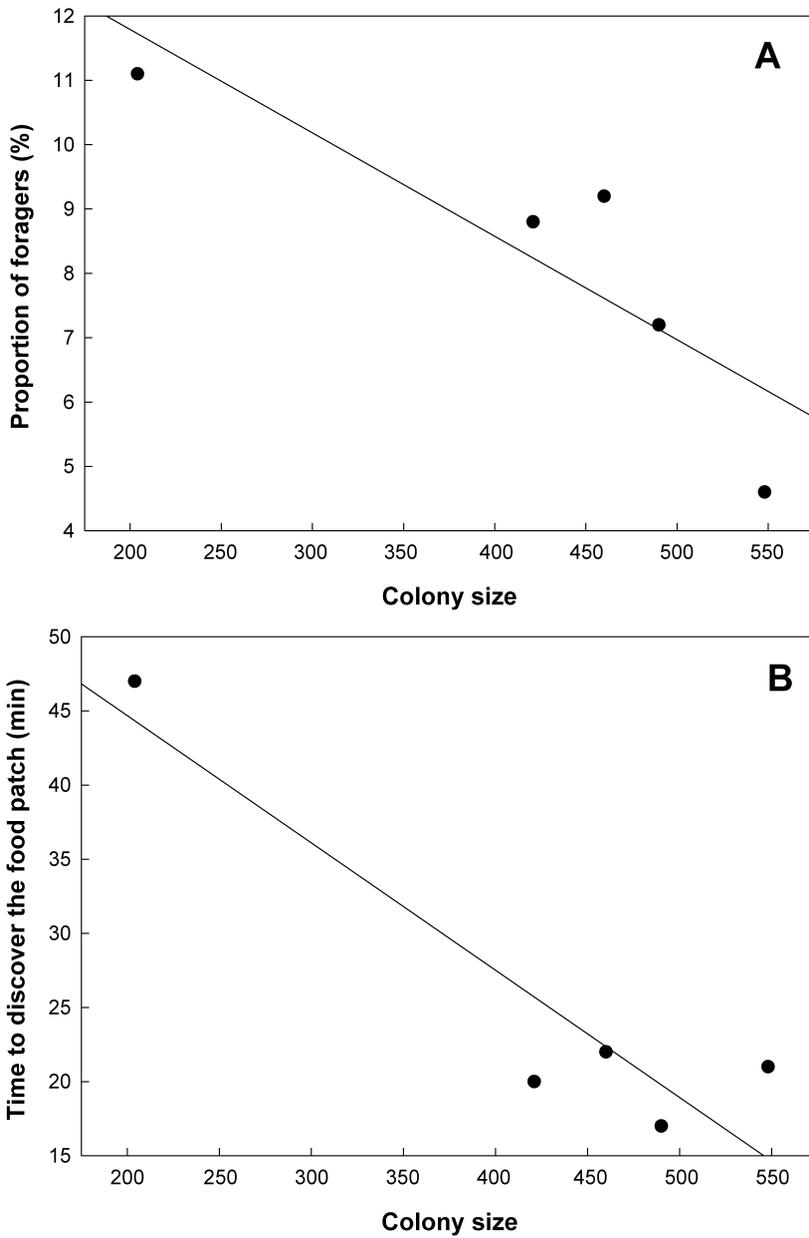
Figure 2. Relationships between colony size (number of individuals of *Pogonomyrmex vermiculatus*) and proportion of foragers (A), and between colony size and time to discover the food patch (B). In both cases, $N = 5$ colonies with pyrazines trails.

Table 1. Results of a two-way ANOVA for the effects of fasting, pyrazines trail, and their interaction on the time to discover the food patch (A) and rate of prey capture (B) by *Pogonomyrmex vermiculatus* colonies.

Source	df	SS	MS	*F*	*p*
(A) Time to food patch (min)					
Fasting	2	860.00	430.00	1.40	0.27
Pyrazines trail	1	1794.13	1794.13	5.83	0.02
Fasting × pyrazines trail	2	89.86	44.93	0.15	0.86
Covariate (colony)	1	36.82	36.82	0.12	0.74
Error	23	7075.26	307.62		
(B) Rate of prey removal (prey items/h)					
Fasting	2	152.60	76.30	2.39	0.11
Pyrazines trail	1	140.83	140.83	4.41	0.04
Fasting × pyrazines trail	2	140.46	70.23	2.20	0.13
Covariate (colony)	1	0.60	0.60	0.02	0.89
Error	23	734.85	31.95		

The colony was utilised as covariate.

The time to discover the food patch was significantly affected by the presence of a pyrazines, but not by fasting nor by the interaction between both factors (Table 1). Foragers discovered the food patch faster in the presence than in the absence of pyrazines (Figure 3A). Similarly, the rate of prey removal was affected by the presence of the pyrazines, but not by fasting nor by the interaction between both factors (Table 1). Ant colonies removed more prey items in the presence than in the absence of the pyrazines (Figure 3B).

Discussion

The effect of fasting on the foraging activity of ants has been demonstrated in numerous studies (e.g., Hölldobler, 1971; Roces & Hölldobler, 1996; Mailleux et al., 2000). The present study shows that after 7 or 21 days of fasting, *P. vermiculatus* colonies allocated after 2 h approx. 25–35 individuals outside of the nest, which is within the range of the work forces displayed by colonies under natural conditions (Torres-Contreras, unpublished data). The low number of individuals assigned to foraging tasks agrees with that documented by Taber (1998) for the nests of South American *Pogonomyrmex*, which are constituted by only a few hundreds of workers. Moreover,
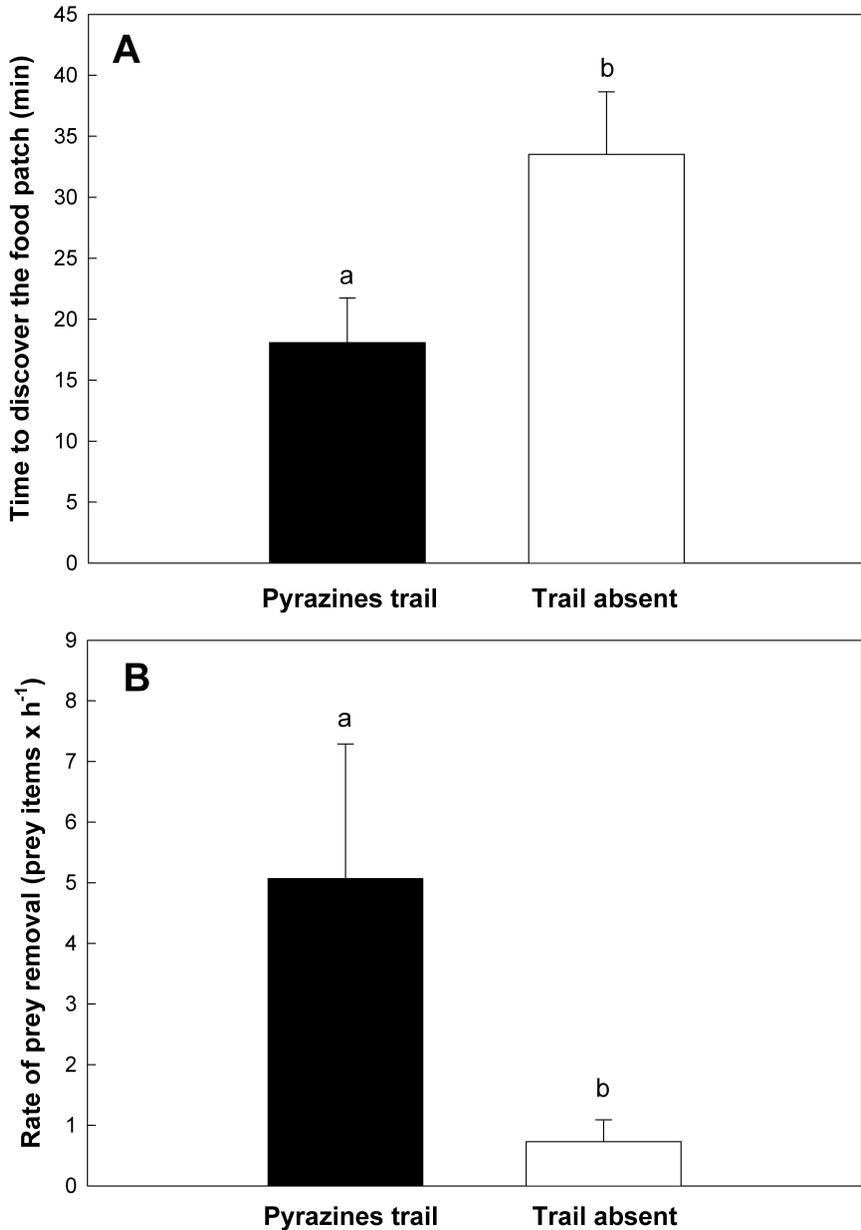
Figure 3. Effect of pyrazines trail on time to discover the food patch (A) and rate of prey capture (B) by *Pogonomyrmex vermiculatus* colonies. Values are mean of 5 colonies (±SE). Different letters above bars indicate significant differences (Tukey a posteriori test, $p < 0.05$). See Table 1 for details.

the number of foragers outside the nest corresponded to ca. 12% of the to-
tal number of ants in the test colony size. This percentage is below the value
found (25%) in other *Pogonomyrmex* species of North America (see Gordon,
1999). This can be attributed to the different foraging strategies (solitary *ver-
sus* group) used by the species.

It has been documented that colonies with a lower number of ants allocate
a greater proportion of workers to foraging activities (e.g., Torres-Contreras
& Vásquez, 2007). This strategy would allow the colony to modulate the
work force outside the nest in response to their nutritional requirements
(e.g., Jaffe & Deneubourg, 1992). It is possible that young colonies (smaller
colonies) allocate a greater proportion of foragers in order to achieve a
greater rate of resource removal and, thus, ensure their growth, development,
and reproduction (e.g., Bourke, 1999). On the other hand, the more individu-
als that are active in a certain area, the faster the information is disseminated
which contributes, for example, to find a food patch (e.g., Detrain et al.,
1999). The shorter time to discover the food patch when the colonies of *P.
vermiculatus* had a greater number of foragers supports that proposal.

The use of communication mechanisms, such as chemical signals, en-
hances the performance of diverse tasks (e.g., nest cleaning, defense pa-
trolling, exploration, and foraging) by the workers that conform a colony
(e.g., Hölldobler & Wilson, 1990; Gordon, 1999). Specifically, different
studies in ants have shown that trail pheromones are involved in behaviours
such as the search, collection and transport of food (e.g., Hölldobler et al.,
2001; Kohl et al., 2001). In particular, in *Pogonomyrmex* species the use of
trail pheromones determines the spatial scale of foraging trajectories through
trunk trails and the efficiency of exploitation of resources with patchy distrib-
ution (e.g., Hölldobler, 1976; Harrison & Gentry, 1981; Crist & MacMahon,
1991; Mull & MacMahon, 1997; Taber, 1998; Hölldobler et al., 2001). Our
results with *P. vermiculatus* support this line of arguments, since the use of
pyrazines trail would allow a colony to discover food faster, to monopolise
food patches present in the habitat, and to increase the rate of resource re-
moval.

It is interesting to note that the number of ants recruited in the sector
with prey was lower than expected by chance in the absence of pyrazines
trail (Figure 1C). This result suggests the occurrence of stress arising from
transporting ants from the field to the lab. Ants are able to judge the quality
of their prey through the scent they produce (e.g., Helmy & Jander, 2003).

An ant recently transported from the field will presumably perceive the prey objects offered as non-attractive.

On the other hand, during the first minutes of the experiment, *P. vermiculatus* workers were found in a greater proportion than expected by chance in the sector with pyrazines trail. However, towards the end of the experiment (ca. 40 min), the proportion of active ants decayed to a value close to that expected by random use of the arena. This time is coincident with the potential active time displayed by alkylpyrazines as trail pheromones (Hölldobler et al., 2001), suggesting that failure to deposit trail pheromones may also be due to stress caused by transport from the field. It is not uncommon that ants under an alarm situation respond by unloading compounds originating from different glands (Hölldobler & Wilson, 1990).

Phylogenetic reconstructions based in chromosomic, morphological, ecological and behavioural (e.g., type of foraging) characters suggests the ancestral nature of South American *Pogonomyrmex* (Taber, 1998). Moreover, the ancestral nature of solitary foraging has been suggested for ants in general (Hölldobler, 1984; Urbani, 1993; Traniello & Robson, 1995) and for *Pogonomyrmex* in particular (Taber, 1998). In North American *Pogonomyrmex*, the derived character 'group foraging' has arisen as a novel behaviour to exploit abundant and patchy resources (Johnson, 2001). In addition, it has been documented that North American *Pogonomyrmex* species (e.g., *P. maricopa*, *P. californicus*) which normally forage in solitary, can display collective foraging when exposed to patches with a high density of food (e.g., Hölldobler, 1976; Davidson, 1977; Crist & MacMahon, 1991; Johnson, 2000, 2001). In *P. vermiculatus*, not only the poison gland accumulates alkylpyrazines that are perceived as trail phreromones by foragers (Torres-Contreras et al., 2007), but also alkylpyrazines are able to recruit foragers and improve the foraging success of ant colonies (this work). This series of evidences suggest that, solitary foraging in *Pogonomyrmex* colonies would show behavioural plasticity when they are under fasting stress and are confronted with abundant resources, probably on account of the opportunistic behaviour of foragers to produce and to use trail pheromones. Preliminary observations at our study site support this proposal. At the beginning of the spring (September of 2006 and 2007), and after three or four months of inactivity, *P. vermiculatus* colonies confronted a great abundance and availability of annual plant seeds (e.g., *Bromus catharticus* and *Stipa plumosa*, both Asteraceae), and were able to display diffuse recruitment and efficient collection of food

(Torres-Contreras, unpublished data). Detailed observations and field experiments are underway to more clearly define the plastic nature of foraging in *P. vermiculatus*.

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