Spatial Heterogeneity and Nestmate Encounters Affect Locomotion and Foraging Success in the Ant *Dorymyrmex goetschi*

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Abstract

The spatial structure of habitats contains physical barriers that restrict the performance of diverse behavioural tasks. In heterogeneous habitats, information acquisition may allow animals to improve the performance of diverse activities such as foraging and locomotion. Nonetheless, changes in locomotion performance and their effects on the foraging success of animals have been scarcely studied. We examined these relationships in the harvester ant *Dorymyrmex goetschi* (subfamily Dolichoderinae) under laboratory conditions. In an experimental arena, we offered a food patch located at a fixed distance from the nest entrance. Landscape heterogeneity was created using wooden cubes arranged in different types of spatial distribution. We video recorded the behaviour of different colonies and quantified the number of active foragers, number of head contacts per capita per inbound trip, path length by workers that transported a food load from the resource patch to the nest, time invested in inbound travels, and the number of prey captured per colony. During the initial phase of patch exploitation, the number of foragers and prey captured were significantly lower than during the half and final phases of the experiment. Landscapes with greater spatial heterogeneity increased travel time and diminished locomotion velocity. A multiple regression analysis revealed that greater antennal contacts and locomotion velocities increased prey removal. Therefore, in this study, we documented a formal link between variables that characterize the movement paths of individuals and the foraging success of a colony. Information transfer between individuals generated a collective work with a concomitant improvement of food exploitation.

Introduction

Heterogeneous habitats cause organisms to experience numerous events of acquisition, transfer and processing of information, which may improve the performance of diverse behavioural tasks such as foraging and movement (Giraldeau 1997; Ydenberg 1998). For example, animals can reduce the amount of errors in their searching time and permanence in a food patch, via experience and/or learning about the location and quality of resources (e.g. Vásquez et al. 2006).

The spatial heterogeneity of the habitat can be expressed as the division of a certain space in favourable (e.g. food patches) and unfavourable (e.g. areas between patches) sites (Southwood 1977). The structure of the landscape, understood as an abstract pattern of organization (e.g. different patch sizes)

and spatial distribution (e.g. distance between patches) (McIntosh 1991), contains physical barriers that restrict the movement trajectories of individuals (Ims 1995; Zollner & Lima 1999). Besides, the spatial heterogeneity experienced by an organism is the product of the interaction between its level of perceptual resolution of the environment and the spatial distribution of environmental constraints (Allen & Hoekstra 1991). The trajectories of individuals that transport a food load in the matrix between a patch and a central place (e.g. nest), can vary during the exploitation time due to the accumulation of experience (e.g. Kolasa & Rollo 1991) and could affect the efficiency of resource harvesting.

During displacements and foraging activities, ants acquire information about the physical characteristics of the habitat and the quality of novel resources (e.g. Adler & Gordon 1992; Roces 1993). For instance, foragers returning to the nest with food can stimulate the recruitment of their nestmates (e.g. Roces 1990; Fourcassié & Traniello 1994). There are several signals (e.g. visual cues, vibratory signals, chemical marks, rate of encounters) by which ants transfer information (see Hölldobler 1999 for a review). For example, antennation between workers scouts and foragers allows decision-making about feeding activities, through physiological and chemical mechanisms of recognition (e.g. Greene & Gordon 2003; Le Breton & Fourcassié 2004). This process may follow simple decision rules (rules of thumb). For example, if a worker at a certain distance and time interval surpasses a threshold value of encounters with nestmate ants performing a given task (e.g. food transportation), this individual will initiate that activity (Gordon 1989; Gordon et al. 1993). On the other hand, structural characteristics of the substratum and the patchy distribution of resources can restrict the movement and foraging success of ants (Crist & MacMahon 1991; Crist & Wiens 1994). For example, an increase of the herbaceous cover diminishes locomotion speeds of harvester ants (e.g. Fewell 1988).

We studied, under laboratory conditions, the changes in locomotion and foraging performance of an ant species when the foragers confront spatial heterogeneity and acquire information from their environment. Laboratory experiments allowed us to eliminate other environmental factors (e.g. temperature, luminosity, competitors, predators) that potentially can interfere with locomotion and foraging behaviour of ants. We asked the following questions: (i) Do activities of workers and resource removal vary with time? (ii) Are movement trajectories affected by spatial heterogeneity? (iii) Do antennation contacts between individuals produce changes in foraging efficiency? (iv) Do trajectories have an effect on food retrieval? We predicted that: (i) the number of foragers and captured prey will increase during the final phase of patch exploitation, (ii) landscapes with greater spatial heterogeneity will increase path length and travel time, (iii) a greater number of encounters among nestmates will increase foraging success, and, (iv) shorter path length and travel times will increase the number of prey captured.

Methods

Study Species and Experimental Arena

The locomotion and foraging behaviour were studied in *Dorymyrmex goetschi* Menozzi 1935, an ant species belonging to the subfamily Dolichoderinae (Snelling & Hunt 1975; Shattuck 1992). The workers of this species have a red coloration in head and thorax, a black abdomen, and a body mass approx. 1.6 mg (Torres-Contreras & Vásquez 2004). These ants construct their nests in open spaces without tree or shrub vegetation. The entrance of the nest has characteristic earth hillocks produced by rubble removed from the interior by the ants. The daily activity of ants begins at dawn with a period of nest cleaning, proceeding afterwards with a period of exploratory and foraging activities. These activities are performed until soil temperature reaches 45°C. At this temperature the entrance of the nest is closed with vegetable material and activities ceases above ground (H. Torres-Contreras, pers. obs.). This species has been documented as belonging to the assembly of harvester ants (Medel & Vásquez 1994; Torres-Contreras 2001). The foraging range of *D. goetschi* colonies commonly cover between 0 and 2.0 m from the nest entrance (Torres-Contreras 2004), but field observations revealed conspicuous variability in locomotion and foraging behaviour of workers at short distances from the nest (i.e. in the range of 10–40 cm; Torres-Contreras & Vásquez, unpubl. data).

During the summer 2002, we identified seven nests of *D. goetschi* in the Rio Clarillo National Reserve (33°51′ S, 70°29′ W), a lower Andes area of central Chile located 45 km SE from Santiago. Our field observations suggest that the colonies comprise a few hundreds individuals, and nests are constructed a few centimetres depth under ground surface, as shown by those nests were the queen was captured (between 30 and 50 cm depth). We extracted

the colonies carefully removing as many workers and larvae as possible, including the queen. We were able to capture the queen of each colony in four out of the seven cases. We found no differences in prey capture and locomotion velocity between colonies with and without queens (Wilcoxon test: $Z = 0.53$, $p = 0.59$; $Z = 1.60$, $p = 0.11$, respectively), and between colonies with different amounts of larvae ($Z = 1.60$, $p = 0.11$; $Z = 0.00$, $p = 1.00$, respectively). Therefore we grouped together the data from all colonies for further statistical analyses.

In the field, colonies were transferred to plastic boxes of $11.0 \times 11.0 \times 5.0$ cm (length × width × height), supplied with four glass tubes of dimensions 1.2×7.5 cm (diameter × length) that contained cotton and water to provide humidity. In the laboratory, ants were acclimatized during 2 wk to their experimental nest and maintained at a constant temperature of 25°C with a 12:12 h light:dark photoperiod cycle. Each colony box was connected to the experimental arena – of dimensions 50.0×50.0 cm (length × width) – by a vinyl tube of 1.0×20.0 cm (diameter × length) that opened at the centre of the arena from below. This area was the maximum feasible in order to allow the acquisition of clear images of ant trajectories. The floor of the arena was made of white melamine-coated wood (1.7 cm thick) and it was marked with a grid of 25 cells of 100 cm^2 each cell. The edges of the arena consisted of translucent Plexiglas walls of dimensions 15.0×0.5 cm (height × thickness). These walls were covered with Fluon to prevent the flight of the ants. Artificial nests were maintained under a closed economy of feeding, that is, workers could obtain food only during the experimental treatments (e.g. McNamara & Houston 1989). Before the experiments, ants had no previous contact with the artificial food items offered during the trials (see below).

Experimental Design

In the field, *D. goetschi* subjects transport natural loads with a mass of 0.97 ± 0.07 mg ($\bar{x} \pm$ SE, n = 506, range: 0.002 – 13.542 mg; Torres-Contreras & Vásquez 2004). In the laboratory experiments, we used compacted sugar microspheres as prey (5.61 ± 0.05 mg, $\bar{x} \pm$ SE, n = 100), which are commercially available. Pilot experiments showed that ants use this food item copiously, as already shown under field conditions (see Torres-Contreras & Vásquez 2004). Although the size of this experimental food was in the upper range of the natural prey distribution of these ants, this size was needed to assure that (i) prey items were detectable from video recordings, and (ii) prey variability was low or nil. Furthermore, prey handling was not affected by those food items (see Torres-Contreras & Vásquez 2004). We offered a food patch with 50 microspheres located at a distance of 20 cm from the nest entrance, and its position was changed at random with respect to the four cardinal points for each experimental treatment. This treatment is representative of resources (e.g. dead small insects) that under field conditions are often distributed at short distances from the nest, and that are exploited by *D. goetschi* ants.

We used wooden cubes of $5.0 \times 5.0 \times 5.0$ cm as objects to manipulate environmental heterogeneity. In any linear dimension, one of those cubes is approx. ten times longer than average ant, and therefore it can limit the free movement of ants. Further, cubes were covered with Fluon, so ants had to circumvent them when confronting them in the arena. An arena without obstacles was used as a control treatment. We used a constant number of 16 cubes that were distributed within the 25 cells of the experimental arena, and we counted the number of cubes contained within each cell. Cells were used as quadrants in order to assess the spatial heterogeneity of objects in the landscape. Following Wiens (1995) statistical criterion, that is, spatial variance (s^2) > 0 to mean heterogeneity, and $s^2 = 0$ to express homogeneity, it was possible to propose a 'measurement of heterogeneity' (*sensu* Kolasa & Rollo 1991) for four landscapes, with the following decreasing order of spatial homogeneity: without obstacles ($s^2 = 0.00$) < objects distributed regularly ($s^2 = 0.24$) < objects distributed at random ($s^2 = 0.33$) < objects with distribution grouped ($s^2 = 0.57$). For each type of landscape the cubes always occupied the same position within the chosen cell. Therefore, there is an unique value of spatial variance for each landscape.

Each colony was subjected to four different treatments of heterogeneity, these being: (i) without distribution (no objects in the landscape), (ii) uniform (uniform distribution of objects in the landscape), (iii) random, and (iv) grouped distribution. Each colony experienced once each distribution in random order. An experiment with one colony per day was carried out, starting at the same hour in the morning (10:00 h). The movement and feeding behaviour of forager workers were recorded with a video camera (Sony CCD-TRV 108; Tokyo, Japan) located 70 cm

above the centre of the experimental arena. This camera had fitted a wide conversion lens 0.6× (Sony VCL-0637H). On an experimental day, a colony box was connected to the experimental arena, and the target colony had access to the arena. When the first ant entered the arena, video recording started, and the behaviour of the colony was recorded during 120 min. For analyses, the exploitation time was divided in three phases of 40 min (initial, half, final) with the objective of evaluating changes in the feeding performance throughout time. After each experiment, the arena was cleaned with a solution of alcohol to eliminate any type of chemical mark left by the workers on the substratum. Videos were watched and the following dependent variables were measured: number of active foragers, number of head contacts per individual per trip, path length by workers that transported one food load (one microsphere in all cases) from the patch to the nest, time invested in inbound travels per ant (hereafter, travel time), and number of captured prey per colony.

A high density of individuals has been correlated with high rates of antennal contacts per ant (e.g. Gordon 1996), and hence with improved decision-making by way of chemical mechanisms of recognition (e.g. Greene & Gordon 2003). We quantified every 5 min the number of foragers present in the experimental arena, and the number of head to head contacts that each worker experienced during its inbound trip. These contacts were used as estimates of information transfer. We followed the methodology and criterion used by Gordon et al. (1993) and Burd & Aranwela (2003) to determine an effective antennal contact between two ants. We quantified, minute by minute, the number of sugar microspheres captured by the colony, and considered a successful removal event when a prey was introduced to the nest by a worker. The movements of individuals between the food patch and the nest were traced in transparent films put directly over a video monitor. These trajectories were scanned and converted to digital images. Path lengths were measured by using SigmaScan SOFTWARE (SPSS Inc., Chicago, IL, USA). We used measurements of distance and duration time of inbound trips to estimate locomotion velocities. The distance, time and velocity of the displacements constitute variables that describe a movement path (e.g. Wiens et al. 1993).

Statistical Analyses

The data were analysed using a protected multivariate analysis of variance for repeated measures.

The method comprises a MANOVA to assess global effects, and repeated-measures ANOVAS if the MANOVA shows significant results (Scheiner 1993). In the ANOVA tests, colony was used as the sample unit, and hence data correspond to the mean of foragers per colony (the range of the number of workers was 4–42 subjects for landscapes without objects; 8–28 subjects for landscapes with uniform distribution of objects; 9–25 subjects for landscapes with random distribution; and 11–25 subjects for landscapes with grouped distribution). Simple linear regressions were used to analyse the relationships between colony size and the proportion of foragers, and between the number of foragers and the number of head to head contacts per capita. The effects of forager number, antennal contacts, path length, travel time, and locomotion velocity on the number of captured prey were analysed with standard multiple linear regressions. All tests were carried out with Statistica 6.0 SOFTWARE (StatSoft Inc., Tulsa, OK, USA). Data shown correspond to the mean of the colonies, and the significance of the statistical tests was set at $\alpha = 0.05$. Data satisfied the assumptions of each test.

Results

The MANOVA showed overall significant main effect for exploitation phase and spatial heterogeneity, whereas the phase by heterogeneity interaction did not have a significant effect (Table 1). We now show the analyses carried out separately for the effect of factors on each dependent variable using two-way repeated measures ANOVAS (see Statistical Analyses).

Exploitation Phase

Independently of the spatial heterogeneity, food patches were discovered (i.e. reached by an ant) after 18.75 ± 2.48 min ($\bar{x} \pm SE$, $n = 28$) from the entrance of workers to the experimental arena, but

Table 1: MANOVA of exploitation phase (initial, half and final; each one of 40 min of duration), spatial heterogeneity, and interaction effects on different dependent variables (number of foragers, path length, travel time, locomotion velocity and captured prey) of the *Dorymyrmex goetschi* foragers

Effect	Wilk's lambda	F	Numerator df	Denominator df	p-value
Phase	0.580	4.255	10	136	<0.0001
Heterogeneity	0.494	3.650	15	188	<0.0001
P × H	0.711	0.811	30	274	0.749

the first successful prey removal occurred at 46.29 ± 2.90 min. We found no differences on discovering times (one-way ANOVA, p = 0.23, df = 3, F = 1.52) nor in the time to the first prey removed (one-way ANOVA, p = 0.57, df = 3, F = 0.69) for different spatial heterogeneities.

The number of active foragers changed significantly with exploitation phase, but not with spatial heterogeneity or the interaction between both factors (Table 2). During the final phase of experimentation, the number of workers (25.57 ± 4.99 subjects, x̄ ± SE, n = 28) was 16% greater that during the half phase (21.54 ± 5.17 subjects), and 50% greater than during the initial phase (12.75 ± 4.06 subjects) (see Fig. 1a).

The number of prey captured by colony was significantly affected by exploitation phase, but not by spatial heterogeneity or the interaction between both factors (Table 2). During the initial phase the

number of food items removed (1.86 ± 1.10 prey, x̄ ± SE, n = 28) was 6.4 times less than during the half phase (13.79 ± 3.75 prey), and 7.6 times less

Table 2: Results of a repeated-measured two-way ANOVA for the effects of exploitation phase and spatial heterogeneity and their interaction on different dependent variables of the *Dorymyrmex goetschi* colonies

| Source	df	SS	MS	F	p-value
No. foragers					
Phase	2	2406.738	1203.369	191.869	<<0.0001
Heterogeneity	3	833.238	277.746	0.886	0.467
Phase × heterogeneity	6	234.402	39.067	1.915	0.105
Error	36	225.792	6.272		
Path length					
Phase	2	620.034	310.017	1.398	0.284
Heterogeneity	3	1197.333	399.111	0.949	0.438
Phase × heterogeneity	6	587.076	97.846	0.639	0.698
Error	36	5510.448	153.068		
Travel time					
Phase	2	830.948	415.474	2.290	0.144
Heterogeneity	3	4218.336	1406.112	7.522	<0.01
Phase × heterogeneity	6	511.278	85.213	0.763	0.604
Error	36	4020.408	111.678		
Locomotion velocity					
Phase	2	0.038	0.019	0.182	0.835
Heterogeneity	3	2.451	0.817	5.024	<0.05
Phase × heterogeneity	6	0.384	0.064	1.852	0.116
Error	36	1.260	0.035		
Prey capture					
Phase	2	3240.666	1620.333	23.328	<0.001
Heterogeneity	3	225.57	75.190	1.224	0.330
Phase × heterogeneity	6	409.998	68.333	0.977	0.455
Error	36	2517.156	69.921		
Per capita capture					
Phase	2	6.138	3.069	19.327	<0.001
Heterogeneity	3	0.468	0.156	0.756	0.533
Time × heterogeneity	6	2.064	0.344	2.275	0.058
Error	36	5.436	0.151		
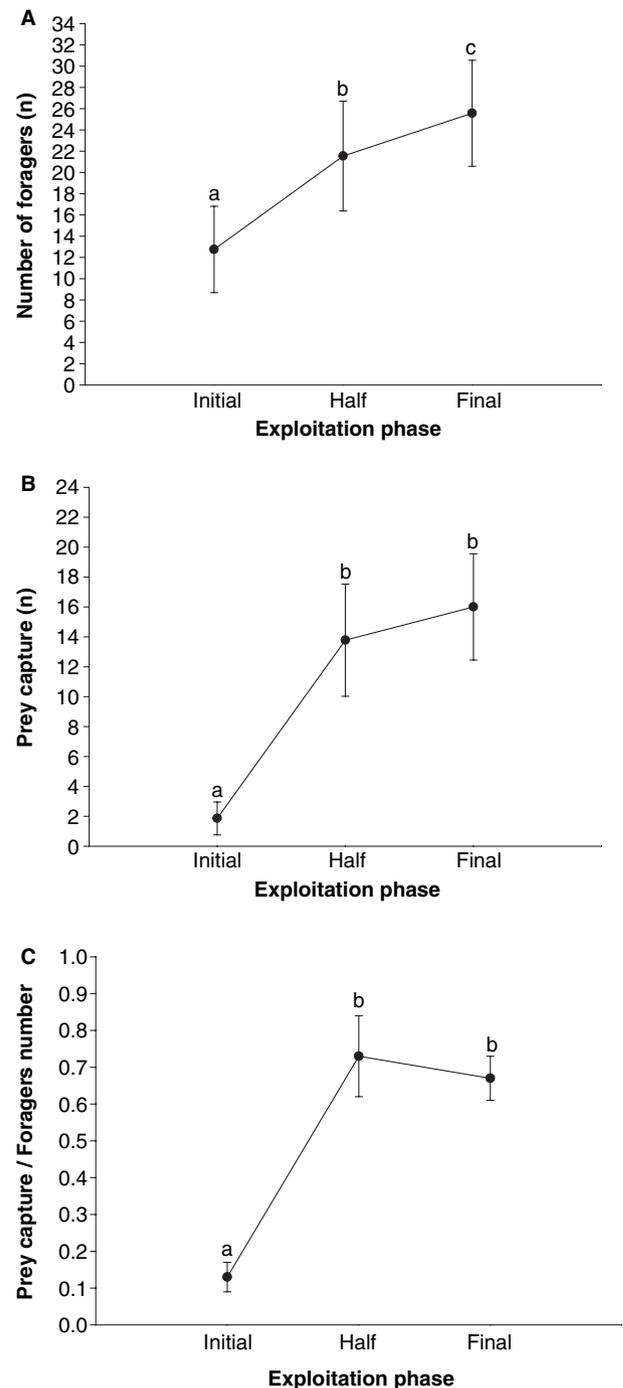
Fig. 1: The effect of exploitation phase on the number of (a) active workers outside the nest, (b) prey capture, and (c) per capita capture by *Dorymyrmex goetschi* colonies. Values are means of colonies (±SE), and different letters above data points indicate significant differences (Tukey test *a posteriori*, p < 0.05). See Table 2 for details

than during the final phase (16.00 ± 3.55 prey) (see Fig. 1b).

The ratio prey capture/forager number was significantly affected by exploitation phase, but not by spatial heterogeneity or the interaction between both factors (Table 2). During the initial phase prey capture per capita (0.13 ± 0.04, $\bar{x}$ ± SE, n = 28) was 5.1 times lower than during the final phase (0.67 ± 0.06 prey), and 5.6 times lower than during the half phase (0.73 ± 0.11 prey) (see Fig. 1c).

Spatial Heterogeneity

The travel time of foragers during inbound trips was significantly affected by spatial heterogeneity, but not by exploitation phase and the interaction between both factors (Table 2). In landscapes with objects distributed at random the time invested (52.64 ± 5.09 s, $\bar{x}$ ± SE, n = 21) was 8% greater than in habitats with obstacles distributed uniformly (48.37 ± 4.23 s), 25% greater than in landscapes with clumped distribution (39.25 ± 3.90 s), and 34% greater than in habitats without obstacles (34.79 ± 5.26 s) (Fig. 2a).

The locomotion speed of foragers during inbound trips was significantly affected by spatial heterogeneity, but not by exploitation phase or the interaction between both factors (Table 2). In landscapes with obstacles distributed at random the velocity (1.06 ± 0.10 cm/s, $\bar{x}$ ± SE, n = 21) was 12% slower than in habitats with objects distributed uniformly (1.19 ± 0.09 cm/s), 26% slower than in landscapes with distribution grouped obstacles (1.34 ± 0.16 cm/s), and 43% slower than in habitats without objects (1.52 ± 0.12 cm/s) (Fig. 2b).

We found no effects of patch exploitation phase, spatial heterogeneity, nor of the interaction between both factors, on path lengths by workers that transported a food load from the patch to the nest (Table 2). The range of path lengths for different experimentation phases was 48.6–55.0 cm, that is, foragers covered 2.43–2.75 times the straight-line distance from patch to the nest. The range of path lengths for different heterogeneities was 47.4–56.5 cm, that is, foragers covered 2.37–2.82 times the straight-line distance from patch to the nest.

Nestmate Encounters and Foraging Success

There was a negative and significant relationship between colony size and percentage of active foragers
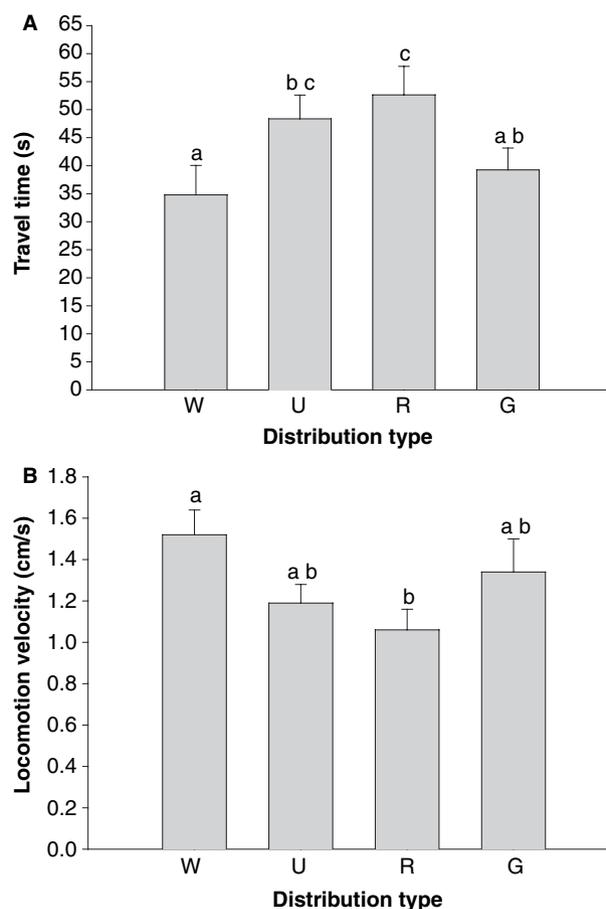

Fig. 2: The effect of spatial heterogeneity (distribution of objects: W, without objects, U, uniform distribution, R, random distribution, G, grouped distribution) on the (a) travel time and (b) locomotion velocity of *Dorymyrmex goetschi* foragers. Values are means of colonies (±SE), and different letters above bars indicate significant differences (Tukey test *a posteriori*, p < 0.05). See Table 2 for details

($r^2 = 0.70$, t = 3.43, p < 0.05; Fig. 3a). On the contrary, there was a positive and significant relationship between the number of active foragers and the number of head contacts per ant per inbound trip ($r^2 = 0.44$, t = 4.53, p < 0.001; Fig. 3b). A multiple linear regression revealed that variables of movement path, forager number and antennal contacts explained a significant fraction (68%) of the variation in the foraging success of colonies (Table 3). Specifically, the antennal contacts and locomotion velocity have a significant and marginally significant effect on the number of captured prey, respectively (Fig. 4). Considering the sign of the parameter estimates (slope), we suggest that larger numbers of antennal contacts and higher locomotion velocities increase prey removal.
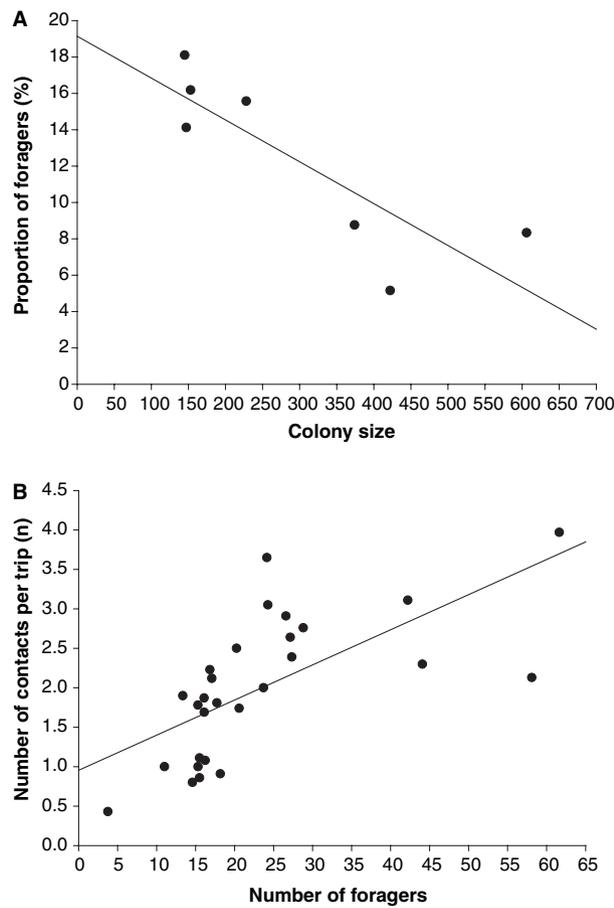
Fig. 3: The relationship between (a) colony size (ant number) and proportion of foragers, and between (b) the number of workers and the number of head to head contacts per capita per inbound trip in *Dorymyrmex goetschi* colonies. Values are means of colonies, and the sample size was n = 7 and n = 28, respectively. See text for details

Table 3: Standard multiple linear regression model on the effect of movement path variables (travel time in s, path length in cm, locomotion velocity in cm/s), number of foragers, and antennal contacts per inbound trip on the number of captured prey by *Dorymyrmex goetschi* colonies

Variable	Slope	Significance
Path length	−0.469	0.259
Travel time	0.194	0.682
Locomotion velocity	28.861	0.092
Forager number	0.170	0.409
Antennal contacts	8.634	0.009
Constant	−11.021	0.675

Regression model summary: $r^2 = 0.68$; $F_{5,22} = 9.38$; $p < 0.0001$

This multiple regression analysis also indicated that the influence of antennal contacts is not merely a result of increased number of foragers.
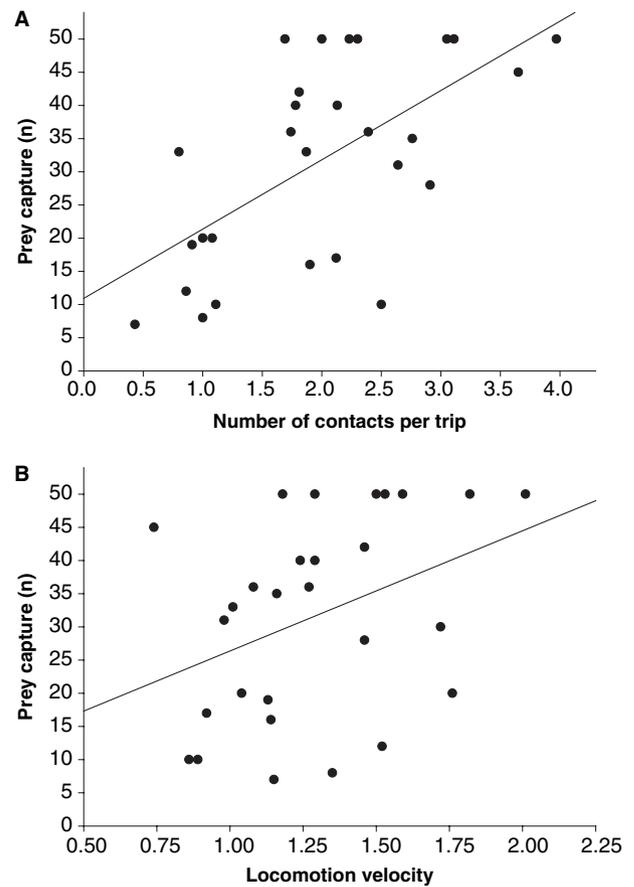

Fig. 4: The relationship between (a) number of antennal contacts per capita per inbound trip and captured prey ($r^2 = 0.38$, t = 3.98, p < 0.001), and between (b) locomotion velocity (cm/s) and number of removed food items ($r^2 = 0.14$, t = 2.06, p = 0.0491) by *Dorymyrmex goetschi* colonies. Values are means of colonies, and the sample size was n = 28. See text for details

Discussion

During the exploitation of a resource patch, there was an increase in the number of *D. goetschi* workers that carried out foraging tasks outside the nest, as found in previous studies (e.g. Beckers et al. 1989; Detrain et al. 1990). The increase in foraging success with time can also be associated to processes of information transfer. Despite the scarce knowledge on the mechanisms of communication in ants of the subfamily Dolichoderinae, we suggest that like other ant species, the chemical sensors through antennation could be the main channel involved in the exchange of information among individuals (see Hölldobler & Wilson 1990). When an ant contacts with its antenna the food transported by a nestmate returning to the nest, it can perceive, through the chemoreceptors located in the tips of the antenna,

the quality of the prey (e.g. Roces 1990; Le Breton & Fourcassié 2004), thus contributing to increase patch finding and exploitation. Furthermore, the arrival rate of successful foragers to the nest prompts further recruitment of workers (Roces & Núñez 1993). Thus, the rapidity whereupon the information is disseminated about new sources of food can have a significant adaptive value for the colony. Saving time in the execution of feeding tasks would allow a colony to monopolize food patches present in the habitat (e.g. Roces 1993).

The smaller number of prey removed during the initial phase of the patch exploitation would be the result of a temporary delay in the decision to accept a novel resource and in the time needed to recruit a certain number of workers. Our observations revealed that once an ant encountered a prey item, a large fraction of the time before prey removal was allocated to be in contact with the prey via its antenna and mouth apparatus for several minutes (up to 20 min approx.), and the remaining time was used in trying to hold the prey (sugar sphere). The use of a novel food item in our experiments seems to have followed this process of resource acceptance as observed from the initial to the second phase of exploitation (see Fig. 1b–c). This result was also supported by the observation that the study species rarely include sugar items in its diet (see Torres-Contreras & Vásquez 2004). As time goes by, the increase in resource removal is linked with a higher number of active foragers (see Detrain et al. 1990; Devigne & Detrain 2002 for other studies with similar results). This augmentation of worker number with time could also increase the chemical signals deposited on the substrate contributing to patch finding and exploitation (see Detrain et al. 1999 for a review).

These results corroborate field data on the effect of information transfer, through antennation affecting foraging success of D. goetschi colonies (H. Torres-Contreras & R.A. Vásquez, unpubl. data). Moreover, an effective exploitation of resources would require that workers use several foraging strategies (e.g. Howard et al. 1996; Detrain et al. 1999). For example, occasionally D. goetschi foragers, like other species of the subfamily, can exhibit mass-recruitment (e.g. Oster & Wilson 1978; Beckers et al. 1989), and display a process of relay with indirect transfer of prey in dump sites (e.g. Ratnieks & Anderson 1999) during the return trips to the nest (H. Torres-Contreras, pers. obs.). In this way, the independent performance of individuals can be integrated in a collective work that allows the colony to make a

more successful removal of resources (e.g. Detrain et al. 1990; Devigne & Detrain 2002). Landscapes with greater spatial heterogeneity increased travel time and reduced locomotion velocity. The magnitude of these variables can have consequences on the fitness of organisms, since a greater time investment outside the nest may increase predation risk (e.g. Feener & Moss 1990), loss of thermal balance (e.g. Lighton & Bartholomew 1988), and/or the missing of information (e.g. Roces & Núñez 1993). It has been documented that for ants it is not so important to maximise the energetic returns but to minimise time investment as a way to maximise the net acquisition of resources in a given period of time (e.g. Fewell 1988; Weier & Feener 1995). The greater number of prey captured by D. goetschi colonies when running speed was faster supports that proposal.

Landscape spatial heterogeneity did not have an effect on foraging success of D. goetschi, although, as mentioned, it did affected locomotion velocity. Since it is biologically reasonable to expect a relationship between locomotion and foraging, we expect that a greater heterogeneity (and/or larger sample size in order to increase statistical power) would significantly affect foraging success. Path length was not affected by exploitation phase nor by spatial heterogeneity. This is possibly due to the fact that individuals marked the trajectories during the initial phase of exploitation, possibly by means of chemical signals. Nevertheless, in the field we found that the inbound travels of this species are more linear with the passing of exploitation time (H. Torres-Contreras & R.A. Vásquez, unpubl. data). Besides, when we calculated a straightness index (see Dejean & Benhamou 1993) that considers the ratio of the distance in straight line from patch to nest (20 cm) divided by the path length, we found smaller ratios, that is more complex trajectories, in the laboratory (0.35–0.42), compared with the field (0.56–0.68) (H. Torres-Contreras & R.A. Vásquez, unpubl. data). This suggests that under natural conditions D. goetschi foragers might use another type of signals during their inbound trips, such as visual and/or celestial signals (e.g. Collet et al. 1992; Akesson & Wehner 2002), which could improve their locomotion performance.

It should be taken into account that under natural conditions ants experience continuous access to their food patches, whereas in our experiments, each colony had a limited temporal access to the food patches (120 min). Therefore, in our experiments, ants could not form a very long-term representation about the heterogeneity of the foraging

environment. Thus, it is possible that our finding of lower values of the straightness index in the laboratory compared with field data is the result of the exposure to a novel environment that does not allow long-term tracking by the ants. Hence, it is possible that the influence of spatial heterogeneity at the scale analysed in the present study could be reduced with longer exploitation experience.

Colonies with a lower number of workers allocated a greater proportion of subjects to foraging tasks. The colonies can modulate the maximum number of foragers outside the nest in accordance with their nutritional requirements (e.g. Jaffe & Deneubourg 1992; Mailleux et al. 2003). For example, young colonies of smaller size need greater resource removal rates to assure growth, development, and reproduction (e.g. Bourke 1999), and hence they might allocate a greater proportion of workers to foraging activities, as suggested by our results. On the other hand, the level of activity exhibited by *D. goetschi* can be conditioned by the composition and predictability of resources. It has been documented that food items rich in carbohydrates present a regular rate of renewal and they provide an important energetic source, which determine a high rate of visits and route fidelity towards feeding sites (e.g. Fresneau 1985; Fourcassié & Traniello 1994).

The relationship found in *D. goetschi* between locomotion velocity and prey capture is a novel finding (see Fig. 4b). Traditionally, locomotion and foraging behaviour have been studied as independent events. Landscape ecology has studied the effects of spatial heterogeneity on the complexity of movement paths (e.g. With 1994), but have not specified the stimulus that triggers movements, the changes that individual trajectories experience throughout time as result of information accumulation, and the influence that locomotion performance can have on other behaviours. On the other hand, studies of optimal foraging have not considered explicitly the movement complexity displayed by the organisms in the matrix between food patches (e.g. Charnov 1976; Stephens & Krebs 1986), and, therefore, they have not analysed the consequences of habitat heterogeneity on feeding performance. In this study, we showed that landscape spatial heterogeneity affects the movement paths of ants (specifically, travel time and locomotion velocity, see Fig. 2), information transfer among workers produces a collective work during the retrieval of food, and documented a formal link between individual trajectories and foraging success of ant colonies.

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