

Research article

A field experiment on the influence of load transportation and patch distance on the locomotion velocity of *Dorymyrmex goetschi* (Hymenoptera, Formicidae)

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Summary. Locomotion velocity during foraging activities is determined by factors such as travel distance, habitat structure and load mass among others. However, few studies on foraging behavior have analyzed the influence of spatial heterogeneity and food transportation on the locomotion velocity of ants under natural conditions. In order to study the mentioned factors, we selected 20 nests of the ant *Dorymyrmex goetschi* (subfamily Dolichoderinae), in a lower Andes locality of central Chile. Half of the nests were offered a food patch located at 10 cm from the nest entrance, and at 20 cm for the other half. We measured the duration of trips between nest and food patch and vice versa, and the distances traveled. We also recorded spatial heterogeneity of the substratum and soil temperature. Temperature was used as a covariate in the statistical analysis. Travel speed was significantly slower when worker ants returned to the nest with a food load, compared to the velocity of foragers without load that traveled from the nest to the patch. When the food patch was located at greater distance, locomotion velocity was significantly faster. Spatial heterogeneity did not affect movement speed. The reduction in locomotion velocity in ants carrying a load of 5.6 mg represents an energetic cost of transportation equivalent to 79% of the costs involved in moving a body mass of 1.6 mg. Faster velocities at larger patch distances can be interpreted as a strategy to maintain an efficient resource exploitation, by way of decreasing the time exposed to higher predation risk.

Key words: Ants, load burden, food patch, spatial heterogeneity.

Introduction

Locomotion velocity is an animal characteristic that determines the performance of other behaviors such as escape

from predators, food searching, and exploration of the environment. In terrestrial arthropods like crabs (e.g., Herreid and Full, 1986b), cockroaches (e.g., Herreid et al., 1981), beetles (e.g., Bartolomew et al., 1985) and ants (e.g., Nielsen et al., 1982), the analysis of this attribute has been centered in the energetic costs and biomechanical aspects associated to pedestrian locomotion. Locomotion velocity can be influenced by habitat structure and food transportation. For example, in hermit crabs, velocity is a function of prey size and substratum, where crabs with lighter load move faster and more efficiently in sand than in rocky substratum (Herreid and Full, 1986a,b).

During the exploration of new areas, ants normally move in a complex form and at low speed, presenting trajectories with high superimposition and larger covered area (Deneubourg et al., 1983; Hölldobler and Wilson, 1990). However, after finding and capturing prey, ants return to the nest with a more linear trajectory and at a greater speed (Johnson, 1991; Herbers and Choiniere, 1996). This behavior would be the result of learning about the location and richness of food patches through the use of familiar marks in the landscape, which would allow workers to reduce their travel and food searching times (Johnson, 1991; Collet, 1996). However, other factors such as nutritional quality of food (e.g., Rocas, 1993), environment temperature (e.g., Marsh, 1985), encounter rates between workers (e.g., Burd and Aranwela 2003), body size (e.g., Burd, 2000), vegetation cover (e.g., Fewell, 1988) and load (e.g., Lighton et al., 1993), can influence locomotion velocity of ants. In particular, areas with high vegetation cover can diminish running speed of harvester ants (Fewell, 1988). On the other hand, although forager ants can carry preys as large as 10–20 times their body weight, transportation of large loads reduces locomotion velocity (Nielsen et al., 1982; Lighton et al., 1987).

There are few studies on foraging behavior under natural conditions that analyze the influence of habitat structure and food transportation on the locomotion velocity of ants. Field

experiments would allow answer the questions: can food patches located at different distances from the entrance of the nest produce changes in locomotion velocity? Is locomotion velocity affected by the load transportation and landscape heterogeneity at low range spatial scale? In this context, the aim of this study was to analyze the effect of resource patch distance, food transportation, and spatial heterogeneity, on the locomotion velocity in a common central Chilean ant. Results are discussed in terms of energetic and time costs that individuals incur during foraging.

Methods

Study site and species

The fieldwork was conducted in the Rio Clarillo National Reserve (33°51' S, 70°29' W), a lower Andes locality of central Chile situated 45 km SE of Santiago. Vegetation is composed mainly by evergreen sclerophyllous woody plants, and annual and perennial herbs (Gajardo, 1993). The climate is a cold temperate regime with precipitation concentrated during the winter and a dry period of about seven months around summer.

The studied species was *Dorymyrmex goetschi* Menozzi 1935, which belong to the subfamily Dolichoderinae (Snelling and Hunt, 1975; Shattuck, 1992). The workers of this species have red coloration in head and thorax, a black abdomen, and a body mass of 1.63 ± 0.01 mg (mean \pm SE, $n = 506$). These ants construct their nests in open spaces without tree or shrub vegetation. The entrance of the nest has a 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 cease above ground (Torres-Contreras, pers. obs.). This species has been documented as belonging to the assembly of harvester ants (Medel and Vásquez, 1994; Torres-Contreras, 2001). Analysis of natural prey transported to the nest shows that this species incorporates insects to its diet in a percentage of 27–47% (Torres-Contreras, unpubl. data). *Dorymyrmex goetschi* constitutes together with *Camponotus chilensis* and *C. morosus*, one of the most common ant species present in the study site (Torres-Contreras, pers. obs.).

Experimental design

The fieldwork was carried out between late October and early December 2001 during the spring season. In the field, *D. goetschi* transport natural loads with a mass of 0.97 ± 0.07 mg (mean \pm SE, $n = 506$, range 0.002–13.542 mg). We used as prey, compacted sugar microspheres (5.6 mg \pm 0.05, mean \pm SE, $n = 100$). Although the size of the experimental food items was in the upper range of the natural prey distribution, this size was needed to assure that (i) prey items were detectable from video recordings, and (ii) prey variability was low or nil. Further, our observations revealed that prey handling was not affected by these prey items. We selected 20 nests of *D. goetschi* to which we offered a food patch of 100 microspheres. To 10 colonies selected at random we placed the food patch at a distance of 10 cm from the nest entrance, and to the other 10 colonies the resource patch was located at a distance of 20 cm. These distances were within the normal foraging range of this species (i.e., 0.0–2.0 m; Torres-Contreras, pers. obs.). Resource patches were set at 8:00 AM and we video recorded (Sony camera, model CCD-TR818) the movement and feeding behavior of forager workers until the resource was depleted and/or the activity stopped. Video records were watched to measure the duration of trips from the nest to

the food patch and vice versa. Subjects moving from the nest to the patch carried no load and were exploring the environment, and subjects moving from the patch to the nest transported one food load per trip (one microsphere in all cases). We could not gather data on ant movement with no-food from the patch to the nest for all colonies, because few subjects returned to nest with no food, and when this happened, subjects moved more erratically (possibly extending their exploratory range), and hence they went outside the video recording area. However, we obtained data on a few colonies showing that ants carrying no food item moving in either direction showed similar speeds ($t = 0.76$, $p = 0.49$, $n = 6$). Therefore, any effect of prey transportation on velocity could be attributable to load. The trajectories of individuals between both points in the space were traced in transparent films put directly over a video monitor. These trajectories were measured by using SigmaScan software (SPSS Inc.). With the measurements of distance and time we estimated average locomotion velocities.

In the field, we measured environmental temperature around each colony at two millimeters above the soil with a digital thermometer (Checktemp, precision ± 0.1 °C). Landscape spatial heterogeneity was estimated with linear transects that were arranged through the matrix that separated the entrance of the nest and the food patch. Following Johnson et al. (1992), we calculated a heterogeneity index that considers the proportion of ground surface covered by some physical element that could inhibit ant locomotion (e.g., stones, twigs, leaves, and/or grass; 2 mm wide and long or larger), in relation to the total surface that include bare ground. For example, if 1 cm is covered by twigs, out of a total distance of 10 cm, then the heterogeneity index has a value of 0.1.

The influence of patch distance, load transportation, and the interaction between both factors on the locomotion speed was analyzed with a two-way ANOVA, with soil temperature used as covariate, and colony as the sample unit. Hence data correspond to the mean of foragers per colony (the range of the number of workers for 10 cm distance was 10–60 for outbound travels and 24–82 for inbound travels; and for 20 cm distance was 7–56 and 11–74, respectively). Simple linear regressions were used to analyze the relationships of soil temperature and landscape heterogeneity with locomotion speed. All tests were carried out with Statistica 6.0 software (StatSoft Inc.). Data shown correspond to the mean \pm one standard error, and the significance of the statistical tests was fixed to $\alpha = 0.05$. Data satisfied the assumptions of each test.

Results

Effect of patch distance and food load

The locomotion velocity of workers without load that travel from the nest to the food patch (outbound direction) and of foragers that transported a food load from the food patch to nest (inbound direction) were: 1.90 ± 0.12 cm/s (mean \pm SE) for outbound to 10 cm distances ($n = 10$ colonies), 1.58 ± 0.13 cm/s for inbound from 10 cm ($n = 10$ colonies), 2.63 ± 0.16 cm/s for outbound to 20 cm ($n = 10$ colonies), and 1.91 ± 0.14 cm/s for inbound from 20 cm ($n = 10$ colonies). The locomotion speed of foragers was significantly affected by patch distance and food transportation, but not by the interaction between both factors (Table 1). Locomotion speed was faster at 20 cm than at 10 cm for both outbound and inbound trips (Fig. 1).

Effect of soil temperature and spatial heterogeneity

There was a positive and significant relationship between soil temperature and locomotion velocity for outbound work-

Table 1. Results of a two-way ANOVA for the effects of resource patch distance and food load and their interaction on the locomotion velocity of *Dorymyrmex goetschi* foragers. The soil temperature (T°) was utilized as covariate

Source	df	SS	MS	F	P
Distance	1	2.069	2.069	7.339	0.011
Load	1	2.274	2.274	8.064	0.008
Distance \times Load	1	0.371	0.371	1.316	0.259
Covariate (T°)	1	7.055	7.055	25.021	<0.0001
Error	33	9.306	0.282		

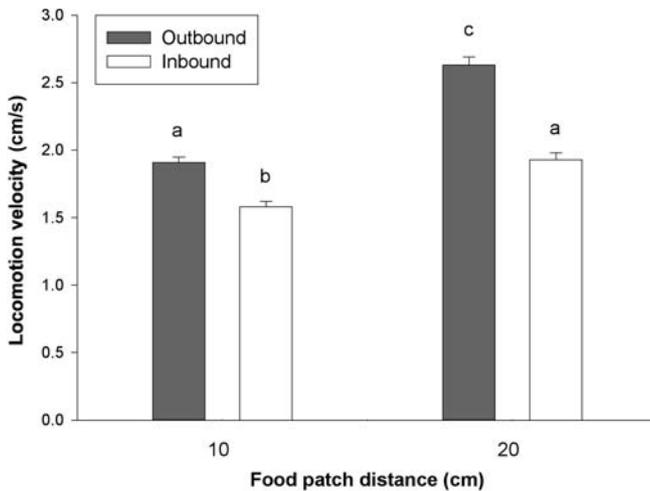


Figure 1. The effect of resource patch distance and food transportation on the locomotion speed of *D. goetschi* foragers. The black bars represent speeds from the nest to the resource patch (outbound direction) and the white bars speeds in the reverse direction (inbound direction). Values are mean \pm SE. Different letters above bars indicate significant differences (Tukey test *a posteriori*, $p < 0.05$)

ers ($r^2 = 0.32$, $t = 2.86$, $p < 0.05$; Fig. 2a). The equation that relates both variables is: $V = 0.56 + 0.06 (T)$, where V corresponds to speed and T is temperature. Similarly, there was a positive and significant relationship between soil temperature and locomotion velocity for inbound foragers ($r^2 = 0.46$, $t = 3.84$, $p < 0.01$; Fig. 2b). The equation that relate both variables is: $V = 0.03 + 0.07 (T)$. On the other hand, there was not significant relationship between landscape spatial heterogeneity and locomotion velocity. Nevertheless, locomotion speed for outbound workers tended to be slower at greater spatial heterogeneity ($r^2 = 0.19$, $t = 2.02$, $p = 0.059$; Fig. 3a). Locomotion speed for inbound foragers was not affected by spatial heterogeneity ($r^2 = 0.10$, $t = 1.38$, $p = 0.186$; Fig. 3b).

Discussion

Foragers of *D. goetschi* were able to transport food loads equivalent to 3.5 times their body mass. One of the immediate effects of food load transportation in ants is the reduction of locomotion velocity (see Fig. 1), which has been attributed to the energetic costs of transportation (Nielsen et al., 1982; Lighton et al., 1987, 1993). In fact, calculations of the minimum cost of transport in ant genera like *Messor* and *Pogo-*

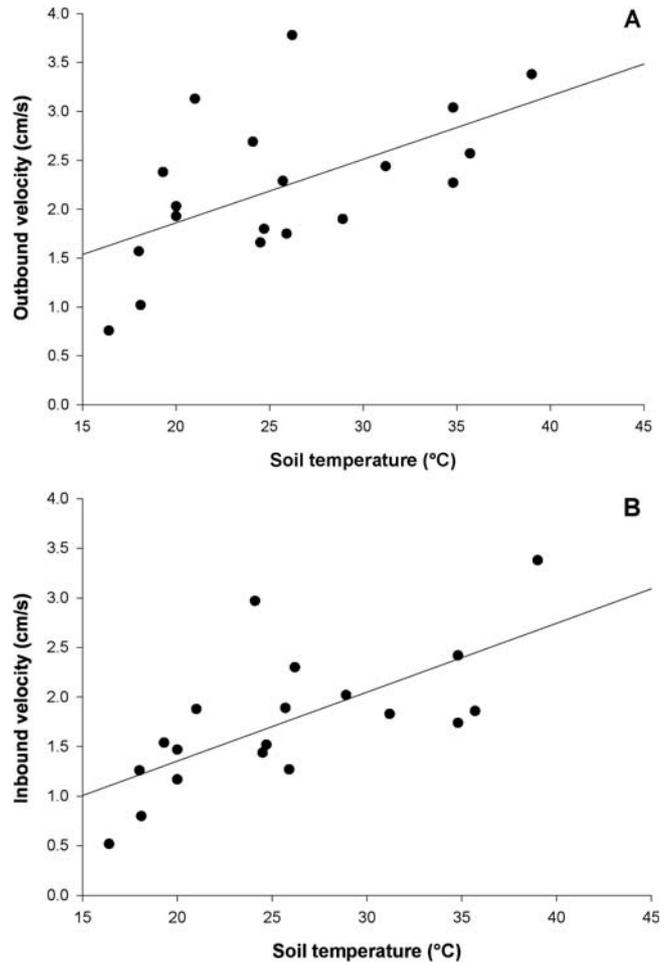


Figure 2. The relationship between soil temperature and mean velocity of *D. goetschi* in outbound (a) and inbound (b) travels. In both cases $n = 20$ colonies. See text for details

nyrmex show that the transportation of a load unit involves an increase of 60% of the energetic costs of locomotion of a unit of body mass (e.g., Nielsen and Baroni-Urbani, 1990; Lighton et al., 1993). Specifically, using equation 5 of Lighton et al. (1993), shows that in *D. goetschi* a load of 5.6 mg, represents a transportation cost of 79% of the cost involved in moving a body size of 1.6 mg. Transportation of loads also produces changes in the spatial pattern of leg coordination in ants, via a reduction of stride length necessary to compensate the forward shift of the center of body mass (Zollikofer, 1994). Therefore, load transportation modifies

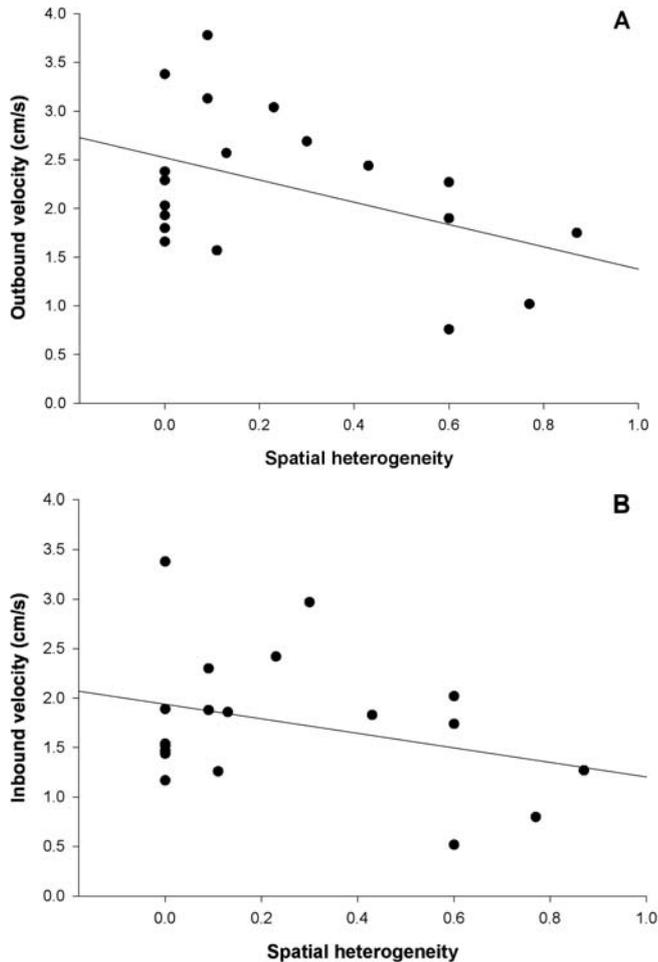


Figure 3. The relationship between landscape spatial heterogeneity and mean velocity of *D. goetschi* in outbound (a) and inbound (b) travels. In both cases $n = 20$ colonies. See text for details

the relative burden over the legs and constrains locomotion velocity (Zollikofer, 1994).

The load burden ($B = M_b + M_l/M_b$, where M_b is body weight and M_l the load mass transported; see Rissing, 1982) of the artificial prey transported in our experiments by *D. goetschi* has a value of $B = 4.5$. This B reduced 25% the locomotion speed of *D. goetschi* foragers. A significant effect of load on locomotion has been reported in different ant species (Nielsen et al., 1982; Lighton et al., 1987, 1993; Burd, 2000). However, for B values between 1.1 and 1.5, locomotion speed is independent of load (Rissing, 1982). We found that natural prey had a $B = 1.6$, which is within the range of B values reported in other studies for harvester ants of the genus *Pogonomyrmex* (Lighton et al., 1993; Weier et al., 1995). Interestingly, this B value implies that *D. goetschi* foragers transport a majority of natural loads that do not seem to modify their speeds, and in this way ants would increase their exploitation rate of resources.

The theory of central place foraging (Orians and Pearson, 1979; Schoener, 1979) predicts that with increasing distance of the resource patch to the nest, an organism will have to

select prey of greater size and/or richer energy content to compensate the energetic costs and time investment involved in traveling greater distances. These models assume that load size does not affect travel time, and hence travel speed (see Wetterer, 1989). Selection of larger and/or more energetic preys has been founded in harvester species of the genera *Pogonomyrmex* (Bailey and Polis, 1987; Crist and MacMahon, 1992; Morehead and Feener, 1998) and *Veromessor* (Rissing and Pollock, 1984), but not in *Messor* (see Baroni-Urbani and Nielsen, 1990). Nevertheless, several authors have suggested that for ants it is not so important to maximize the energetic returns but to minimize time investment, and thus to maximize the net acquisition of resources in a certain period of time (Fewell, 1988; Weier and Feener, 1995). In this study, prey size was the same for both distances, thus the increase in locomotion speed at longer distance cannot be attributable to load carriage only (see Wetterer, 1989), and can be interpreted as a strategy that tend to maintain an efficient resource removal rate, particularly if other costs increase with distance and/or time exposed outside the nest. For example, decreasing the time involved in trips to and from the nest for longer distances may allow ants to maintain a certain level of predation risk, when this risk increases with distance from the nest (Feener and Moss, 1990). In fact, it has been observed that animals move faster under higher predation risk (Vásquez et al., 2002). In our study, ants might have experienced higher predation risk at longer distances from the nest, and therefore they might benefit by traveling faster to and from more distant patches. On the other hand, a higher encounter rate of foragers could also diminish locomotion speed due to interference during movement (Burd and Aranwela, 2003). If encounter rate is higher closer to the nest, as it would be expected, then speeds would be slower at shorter distances from the nest, as it was our case.

Our results show that *D. goetschi* is not a termophilic species, because the temperatures where the workers displayed activities were in the range of 14–42°C. Despite that during the course of experimental trials temperature increased steadily and hence contributed to increasing locomotion speed, higher velocities might also be the result of information processing at individual and colonial level (e.g., Johnson, 1991; Wehner et al., 1996). In laboratory experiments at constant environmental temperature, the movement speed of *D. goetschi* foragers is greater during the final phase of resource exploitation, probably due to the use of familiar landmarks in the landscape and/or chemical signals (Torres-Contreras and Vásquez, unpubl. data).

Several studies have found that increases in the complexity of movement are determined by the physical barriers that the landscape impose to the trajectories of organisms (e.g., With, 1994; Wiens et al., 1995). We have found that increases in habitat spatial heterogeneity produces movement paths with a more complex shape, that is, trajectories with high superimposition and greater fractal dimension (Torres-Contreras and Vásquez, unpubl. data). In this study, spatial heterogeneity did not affect locomotion velocity, which could be the result of changes in time expenditure during locomotion.

Possibly, ants compensate an increase in trajectory sinuosity with faster movement. Therefore, it seems that when the temporal dimension is added to the spatial analysis of movement, the effect of landscape heterogeneity is not conclusive. The influence of habitat heterogeneity on the locomotion velocity can affect other behaviors. For example, fieldwork and laboratory experiments with *D. goetschi* have shown lower resource removal rates when confronted with a greater proportion of physical barriers in the landscape (Torres-Contreras and Vásquez, unpubl. data). Future studies should consider the stimuli that trigger movement decisions (e. g., food), the temporal dynamics of movement (e. g., information acquisition) and the implications on other behaviors (e. g., foraging efficiency), for a proper understanding of the influence of habitat structure on the locomotion of animals.

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