Effect of Colony, Patch Distance, And Trajectory Sense on Movement Complexity in Foraging Ants

Hugo Torres-Contreras · Mauricio Canals

Abstract Animals display foraging trajectories when exploiting food patches. These displacements have been studied, particularly in organisms that forage from a central place. The complexity of a movement path may be analyzed by means of the fractal dimension, an index that estimates the tortuosity of a trajectory. In field experiments we studied the effect of trajectory sense, distance to the resource patch and colony on the movement complexity in a common ant of central Chile. We found that these factors and their interactions significantly affected the complexity of movement paths. We discuss whether mortality risk determines more linear trajectories when the resource patch is distant from the nest, and whether the information acquired from the environment by workers determines less complex return trips.

Keywords *Dorymyrmex goetschi* · movement path · fractal dimension · distant patch · inbound trajectory

Introduction

Locomotive behavior has implications on the fitness of organisms. Locomotive displacement allows, for example, search for refuges, mates and food for satisfying the energetic and nutritional demands of the individuals (e.g. Bell 1990; Krebs and Davies 1993; Wehner 1997). Displacements during daily activities involve home ranges from a few to hundreds of m^2, and are therefore navigation phenomena on a medium and small scale (e.g. Wehner 1996; Sherry 1996; Collet 1996a, b). Animals display foraging trajectories when exploiting food patches (e.g. Charnov 1976; Stephens and Krebs 1986). These displacements have been studied, particularly in organisms that forage from a central place, that is, in

H. Torres-Contreras (✉) · M. Canals
Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile
e-mail: htoresco@uchile.cl

individuals that after capturing prey transport them to a fixed central place (e.g. nest) where they consume it, store or provide food to progeny (Orians and Pearson 1979; Schoener 1979).

One way to study the displacement of organisms is to analyze their movement paths, which correspond to the spatial trajectory of individuals from one locality to another during a period of specific time (Turchin et al. 1991). In particular, these trajectories may be studied by means of simple descriptors such as displacement length, turn angle, and movement sense (e.g. Müller and Wehner 1988; Wallim and Ekbom 1988; Wiens et al. 1993; Collet et al. 1998), using adjustments to models and/or mathematical simulations such as diffusion and random walk (e.g. Kareiva and Shigesada 1983; McCulloch and Cain 1989; Bell 1991; Johnson et al. 1992), and fractal tools such as fractal dimension (e.g. Sugihara and May 1990; With 1994b; Wiens et al. 1995; but see Turchin 1996, 1998), among others.

Specifically, the complexity of a movement path may be analyzed by means of the fractal dimension, an index that estimates the tortuosity of a trajectory. The fractal dimension of a displacement on a plane in two dimensions can take values between 1.0, which correspond to linear trajectories (i.e. straight), and 2.0, which correspond to chaotic movements that present a higher overlap covering a large surface (Burrough 1981; Mandelbrot 1983; With 1994b; Wiens et al. 1995; Turchin 1996). The calculation of the fractal dimension is based on the following relation:

$$L(\delta) = K\delta^{1-D}$$

where L represents the length of a movement path, δ is the scale or rule of measurement, K is the intercept of the regression line, and D corresponds to the fractal dimension (Mandelbrot 1983; Sugihara and May 1990; With 1994b). Specifically, fractal dimension can be derived from the regression of ln L on ln δ and the equation $D = 1-b$, where b is the slope of the regression (Dicke and Burrough 1988; With 1994b; Turchin 1996). Fractal analysis provides a scale-independent measurement that can be used to determine the structure of movement patterns across a range of scales (Sugihara and May 1990; With 1994a; Wiens et al. 1995; but see Turchin 1996, 1998).

Ants are central-place foragers that transport single food loads (Harkness and Maroudas 1985; Bailey and Polis 1987) and exhibit highly variable trajectories (Leonard and Herbers 1986; Gordon 1994). Ants exhibit a great movement complexity compared to other insects and vertebrates (Fourcassie et al. 1992; Wiens et al. 1995). During the exploration of new areas, ants move in complex patterns, presenting trajectories with high overlap and large area covered (Deneubourg et al. 1983; Hölldobler and Wilson 1990). However, it has been proposed that after finding and capturing prey, ants return to the nest following more linear trajectories (Johnson 1991; Herbers and Choiniere 1996). The aim of this study was to analyze -in field experiments- the effect of trajectory sense, distance to the resource patch and colony on the movement complexity in a common ant of central Chile. We predicted that outbound trajectories and distant food patches will increase the complexity of movement paths, and expected high variability in the values of the fractal dimension between colonies.

Methods

Study Site and Species

The fieldwork was conducted in the Rio Clarillo National Reserve (33° 51′ S, 70° 29′ W), in the foothills of the Andes of central Chile, 45 km SE of Santiago. Vegetation is mainly composed of 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.

The studied species was *Dorymyrmex goetschi* Menozzi 1935, which belongs to the subfamily Dolichoderinae (Snelling and Hunt 1975; Shattuck 1992). The workers of this species have a red coloration on the head and thorax, a black abdomen, and a body mass of about 1.6 mg (Torres-Contreras and Vásquez 2004). Nests contain an average of 297±67 workers (mean±SE, n=7 colonies). These ants construct their nests in open spaces without tree or shrub vegetation. The nest entrance 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, followed by a period of exploratory and foraging activities. Ants of this species exhibit mainly solitary foraging but sometimes present diffuse group recruitment (Torres-Contreras and Vásquez 2007). This activity is performed until the soil temperature reaches 45º C. At this temperature the entrance of the nest is closed with vegetable material and above-ground activities cease (Torres-Contreras 2004). This species has been documented as belonging to the assembly of harvester ants (Medel and Vásquez 1994; Torres-Contreras 2001). However, analysis of natural prey transported to the nest showed that this species includes 37% insects in its diet (Torres-Contreras 2004). The foraging range of *D. goetschi* colonies commonly covers between 0 and 2.0 m from the nest entrance, but field observations revealed conspicuous variability in locomotion and foraging behavior of workers at short distances from the nest (i.e. in the range of 10–40 cm; Torres-Contreras, unpubl.data).

Experimental Design

The fieldwork was carried out during the spring of 2002. In the field, *D. goetschi* workers transport natural loads with a mass of 0.97±0.07 mg (mean±SE, n=506, range 0.002–13.542 mg; Torres-Contreras and Vásquez 2004). We used commercially available compacted sugar microspheres as prey (5.61 ± 0.05 mg, mean±SE, n=100). Although the size of this experimental food was in the upper range of the natural prey size 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. Further, prey handling is not affected by those food items (see Torres-Contreras and Vásquez 2004). We selected 9 natural nests of *D. goetschi* to which we offered a food patch of 100 microspheres at two different distances, near (10 cm) and far (20 cm), from the nest entrance. Sugar pellets constitute a single patch with contagious distribution, which was located on bare soil and offered in one of the different directions that are used by the colonies. In addition, we quantified the number of prey removed as a measure of

foraging success. A removal event was considered successful when a prey was introduced to the nest by a forager. Each colony experienced each distance once, in random order. Resource patches were set at 8:00 AM and we video recorded (Sony camera, model CCD-TR818) the movement and feeding behavior of foraging workers until the resource was depleted and/or activity stopped.

Videos were studied and the trajectories of workers without loads that traveled from the nest to the food patch (outbound direction) and of foragers that transported a food load from the food patch to the nest (inbound direction), were drawn. 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. Specifically, the movement paths were traced on transparent film placed directly over a video monitor. These trajectories were scanned and converted to digital images (bmp), using a standard format framing the trajectories between the nest entrance and the food patch (following Canals et al., 2000, 2005). Images were then studied using the Paint Shop Pro[R] software to eliminate all structures except the movement path. Each image was individually analyzed and its fractal dimension (D) computed by the box-counting method, with Benoit[R] v1.2 software. Finally, we registered -in seconds- each of the trajectories displayed by workers, with the objective of evaluating changes in movement complexity over time.

Statistical Analysis

Previously, the data of fractal dimension (D) were transformed with the Box-Cox transformation of logD ($\lambda=1.5$) (Box and Cox 1964, and also see e.g. Angilletta et al. 2008) in order to satisfy the ANOVA assumptions. A three-way ANOVA was carried out to evaluate the effect of colony, resource patch distance, and trajectory sense on the complexity of movement paths. The time taken in that trajectory was used as covariate. ANOVA tests were carried out with Statistica 6.0 software (StatSoft Inc.). A correlation analysis was carried out between fractal dimension of trajectories and number of prey captured. Data shown in figures correspond to the mean of the colonies, and the significance of the statistical tests was set at $\alpha=0.05$.

Results

Complexity of the movement paths was significantly affected by colony, patch distance, trajectory sense and interactions between factors (Table 1). Specifically, there was a high variability in the values of the fractal dimension between colonies (range: 1.126–1.231), trajectories were more complex in resource patches near the nest entrance (1.226±0.001 *versus* 1.154±0.003, for food patches 10 and 20 cm distant, respectively; Fig. 1a), and trajectories of return to nest exhibited less complexity (1.220±0.002 *versus* 1.164±0.003 for outbound and inbound trajectories, respectively; Fig. 1b). With respect to the interaction between factors, we did not find differences in movement complexity for outbound trajectories to different patch distances (1.222 ± 0.002 *versus* 1.236±0.002, for food patches 10 and 20 cm distant, respectively; Fig. 2a), but inbound trajectories were less complex from

Table 1 Results of a Three-Way ANOVA for the Effects of the Colony, Patch Distance, Trajectory Sense and Their Interactions on the Fractal Dimension (transformed with Box-Cox, see text) of Movement Paths by *Dorymyrmex goetschi* Forager Ants

Source	df	SS	MS	F	p
Colony	8	0.00637	0.00080	102.0	<< 0.001
Patch distance	1	0.01077	0.01077	1377.0	<< 0.001
Trajectory sense	1	0.00690	0.00690	881.0	<< 0.001
Colony x distance	8	0.00056	0.00007	9.0	<< 0.001
Colony x sense	8	0.00032	0.00004	5.0	<< 0.001
Distance x sense	1	0.00866	0.00866	1107.0	<< 0.001
Colony x distance x sense	8	0.00059	0.00007	10.0	<< 0.001
Covariate (time)	1	0.00001	0.00001	1.0	0.396
Error	1316	0.01030	0.00001		

greater distances (1.218 ± 0.002 *versus* 1.095 ± 0.002 for food patches 10 and 20 cm distant, respectively; Fig. 2b). The analysis of correlation between fractal dimension and preys captured was not significant ($r^2=0.01$, $t=0.32$, $p=0.76$, for near distance and outbound sense; $r^2=0.15$, $t=1.12$, $p=0.30$, for near distance and inbound sense; $r^2=0.10$, $t=0.89$, $p=0.40$, for far distance and outbound sense; $r^2=0.10$, $t=0.89$, $p=0.40$, for far distance and inbound sense; $n=9$ colonies for all cases). The number of prey removed per colony varied between 11–74 and 10–72 for short and long distances, respectively.

Discussion

The colonies of social insects exhibit a high degree of variation in the expression of behaviors (Gadau and Fewell 2009; Hölldobler and Wilson 2009). In ants, changes in the allocation to specific tasks and activity level during foraging appear to be associated with ecological and genetic factors (e.g. Gordon 1996, 1999; Ingram et al. 2005; Wiernasz et al. 2008). In this context, the variability in movement complexity of the workers would be a consequence of the habitat heterogeneity and/or genetic variability among colonies, and therefore correlated with a differential performance during the exploitation of resource patches. However, we did not find any signification correlation between number of prey captured and the fractal dimension of the movement paths. Previous reports showed that work force, recruitment system, and cooperative strategies are the main factors directly involved in the successful foraging of ants (e.g. Beckers et al. 1989; Detrain et al. 1999; Ratnieks and Anderson 1999).

An important factor that affects the foraging behavior of ants is mortality risk (e.g. Nonacs 1990). The habitat associated with distant resource patches represents a more dangerous area that determines, for example, a lower recruitment (e.g. Nonacs and Dill 1988, 1990). In this study, we found that resource patches located at greater distances from the nest entrance diminish the value of the fractal dimension of the foraging trajectories. Previously, we reported an increase of locomotion velocity in
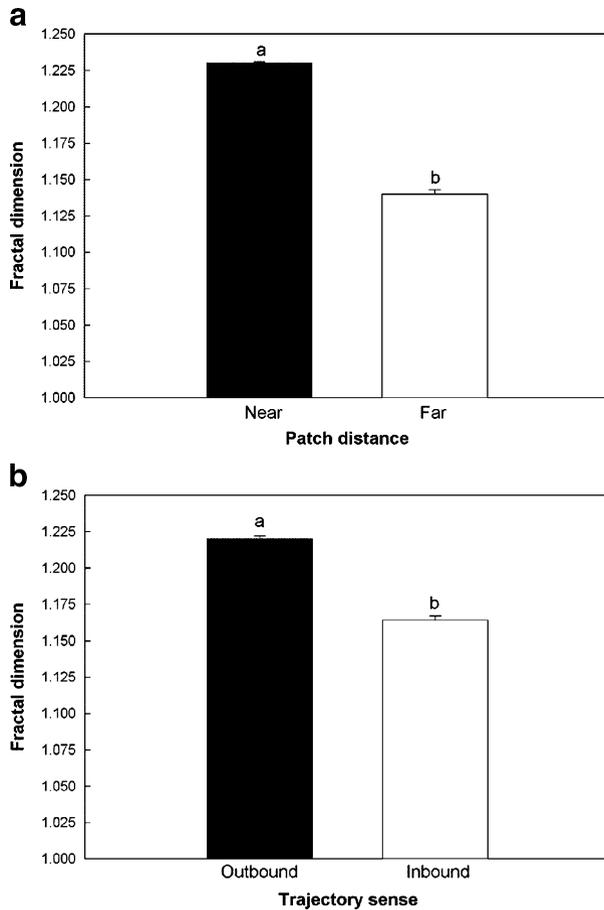
Fig. 1 Effect of the resource patch distance **a** and trajectory sense **b** on the fractal dimension of foraging displacements by *Dorymyrmex goetschi* ants. Values are mean of 9 colonies (± SE). Different letters above bars indicate significant differences (Tukey *a posteriori* test, $p<0.001$). See Table 1 for details.

this species when the food patch was more distant (Torres-Contreras and Vásquez 2004). Both variables can have consequences on the fitness of organisms, since a lower time investment outside the nest may diminish predation risk (e.g. Feener and Moss 1990), loss of thermal balance (e.g. Lighton and Bartholomew 1988), and/or the missing of information (e.g. Roces and Núñez, 1993). Moreover, in this study and previous work (e.g. Torres-Contreras and Vásquez 2007) we have found that travel times and locomotion velocity did not change during the exploitation phases of the food patch. On the other hand, a higher encounter rate of foragers could also increase movement complexity due to interference during movement (see e.g. Burd and Aranwela 2003). If encounter rates are higher closer to the nest, then trajectories would be more tortuous at short distances from the nest, as they were in our case (see e.g. Torres-Contreras and Vásquez 2004). However, it is also possible that the trajectories of return from distant patches during their final tour (last 10 cm) shows movements as sinuous as those in nearby patches.
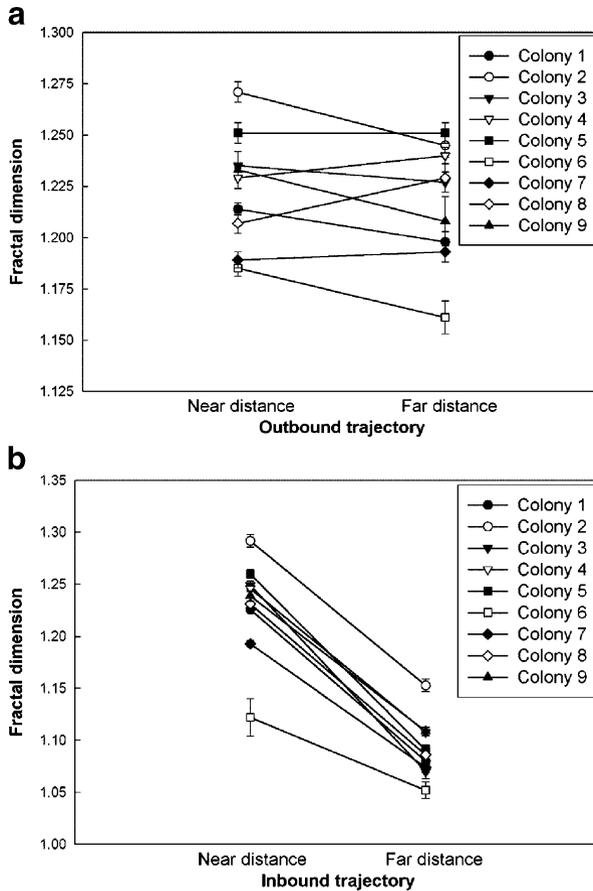
Fig. 2 Effect of the interactions between colony, patch distance and outbound trajectory **a** and colony, patch distance and inbound trajectory **b** on the fractal dimension of foraging displacements by *Dorymyrmex goetschi* ants. Values are means of 9 colonies (± SE). See Table 1 for details.

The inbound trajectories of *D. goetschi* workers were more linear than outbound displacements. This suggests that this species acquires and uses information from its environment during patch exploitation. There are different mechanisms for interchange and transfer information in ants, as for example, visual cues, vibratory signals, chemical marks and rate of encounters (e.g. Hölldobler and Wilson 1990; Hölldobler 1999). In particular, we have documented that antennal contacts between workers improve the foraging success of *D. goetschi* colonies (Torres-Contreras and Vásquez 2007). It is also possible that during their inbound travels *D. goetschi* foragers use another type of signal, such as visual and/or celestial signals (e.g. Collet et al. 1992; Akesson and Wehner 2002), which could improve their locomotion performance. Specifically, the diminution in complexity of inbound trajectories may be interpreted as a strategy of spatial navigation, which allows the avoidance of obstacles in the space (e.g. Collet 1996c; Wehner et al. 1996) and the maintenance of an efficient resource removal rate (see e.g. Torres-Contreras and Vásquez 2007).

The tortuosity of the movement paths through time in *D. goetschi* foragers constitutes a random walk response. This pattern is the most profitable search strategy for taxa that confront a novel environment and have uncertainty about behavior such as patch exploitation (Zollner and Lima 1999; Viswanathan et al. 1999; Bartumeus et al. 2005). In this study, we highlighted the importance of resource location and experience acquired by workers during their foraging trips on the tortuosity of movement paths. Future research should focus on knowing if the intercolony variability in movement complexity is determined by extrinsic ecological factors (e.g. microclimate, vegetation structure, resources spatial distribution, natural enemies; Crist and MacMahon 1991; Crist and Haefner 1994; Crist and Wiens 1994; Wiens 1995), and/or intrinsic biological factors (e.g. age, size, nutritional state, genetic variability of the colonies; Wilson 1985; Houston et al. 1988; Gordon 1995; Ingram et al. 2005).

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