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An empirically based simulation of group foraging in the harvesting ant, *Messor pergandei*

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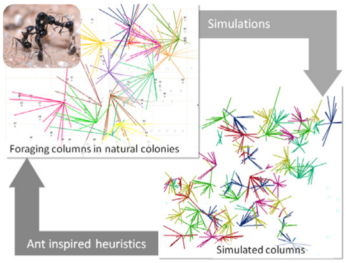
HIGHLIGHTS

- Empirically based group model of foraging interactions in column foraging ant.
- *Messor pergandei* ants balance column length with costs of aggressive interactions.
- Influence of behavioral strategy, nest distribution and density on foraging dynamics.

GRAPHICAL ABSTRACT



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ABSTRACT

We present an empirically based group model of foraging interactions in *Messor pergandei*, the Sonoran desert harvesting ant. *M. pergandei* colonies send out daily foraging columns consisting of tens of thousands of individual ants. Each day, the directions of the columns may change depending on the resource availability and the neighbor interactions. If neighboring columns meet, ants fight, and subsequent foraging is suppressed. *M. pergandei* colonies face a general problem which is present in many systems: dynamic spatial partitioning in a constantly changing environment, while simultaneously minimizing negative competitive interactions with multiple neighbors.

Our simulation model of a population of column foragers is spatially explicit and includes neighbor interactions. We study how different behavioral strategies influence resource exploitation and space use for different nest distributions and densities. Column foraging in *M. pergandei* is adapted to the spatial and temporal properties of their natural habitat. Resource and space use is maximized both at the colony and the population level by a model with a behavioral strategy including learning and fast forgetting rates.

1. Introduction

Many animals defend territories, including social insects such as bees (Wainwright, 1978; Breed et al., 2002), ants (Hölldobler and Wilson, 1990, 2009), and termites (Adams and Levings, 1987). Social insects are particularly interesting because territory boundaries arise from distributed decision making processes. In addition, partitioning of space between neighbors emerges from decisions made by multiple groups. Classification of territoriality in ants is based on temporal and spatial components (Hölldobler and Lumsden, 1980). When a territory persists over space and time, it is referred to as "absolute," e.g., Adams (1998, 1990), Brian et al. (1967), Brian and Elmes (1974), Plowes and Adams (in preparation) but when the territory is transient, it is referred to as "spatio-temporal." Spatio-temporal territories are those in which only the

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actively foraged area is defended against conspecifics e.g., Hölldobler (1974), Whitehouse and Jaffe(1996), Hölldobler (1981). The large majority of models of territoriality in social insects have described absolute territoriality e.g., Hölldobler and Lumsden (1980), Adams (1998, 1990). In this paper we describe a group level simulation model of spatio-temporal territoriality in *Messor pergandei*, a common harvesting ant in the Sonoran desert (Tevis, 1958; Gordon, 1978; Wheeler and Rissing, 1975; Rissing and Wheeler, 1976; Rissing and Pollock, 1989). Colonies of *M. pergandei* send out daily foraging columns consisting of tens of thousands of ants. Each day, colonies can change the direction of columns e.g., Wheeler and Rissing (1975), Rissing and Wheeler (1976), Rissing and Pollock (1989), and when neighboring columns intersect, fights break out between colonies (Wheeler and Rissing, 1975; Went et al., 1972) (Fig. 1).

A simple self-organized, individual behavior based model describing the formation and movement of columns in *M. pergandei* was developed by Goss and Deneubourg (1989). The major premise behind this model was that foraging columns 'rotated', like the hands of a clock, on subsequent foraging bouts (Wheeler and Rissing, 1975; Rissing and Wheeler, 1976; Rissing and Pollock, 1989; Went et al., 1972; Bernstein, 1975). In this model, individual behaviors incorporated include foragers laying trails when returning to the nest, and foragers following a simple rule of choosing the most heavily marked trail when leaving the nest. The foraging area is divided into sectors which start out with similar abundances of food. Positive feedback via differences in pheromone concentration results in increased recruitment to one sector. As a sector's food supply diminishes through foraging, the relative abundance of preferred food types is higher in neighboring sectors, and foraging shifts to the adjacent sector. Thus the foraging trail shifts incrementally, sweeping across the foraging area as food supplies decrease, like the hands of a clock. The model does not include the effect of neighbor presence, nor can it explain how or why changes in column direction do not follow a predictable clockwise pattern of movement (Plowes et al., 2013) or what causes colonies show preferences for certain foraging locations (Gordon, 1978; Plowes et al., 2013). Columns in natural colonies extend and retract at each foraging bout (once or twice a day depending on the season) (Plowes et al., 2013).

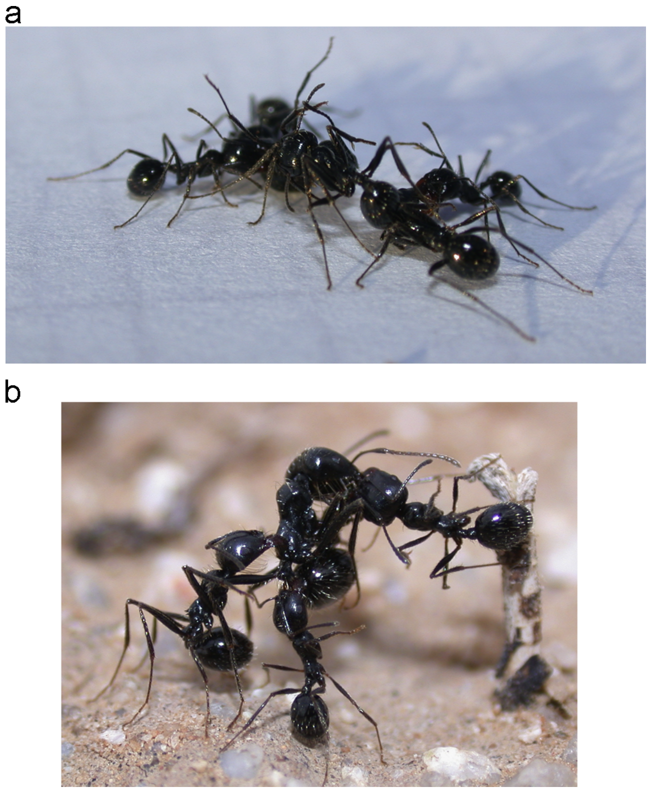

Fig. 1. We used the presence of aggressive behavior between individual ants to ascertain whether columns had intersected or not and were interacting with each other. (a) Individual ants from different *M. pergandei* colonies can be induced to display aggressive behavior by placing individuals from neighboring nests in a small arena. (b) Naturally observed aggressive behavior includes immobilization followed by biting.

Alternative hypotheses for the function of foraging columns include both food acquisition and defense of resources (Ryti and Case, 1984, 1986, 1998). In many territorial ants, aggressive encounters have a role in establishment and maintenance of foraging areas (Adams, 1990; Hölldobler, 1974; Mabelis, 1979). Previous studies in *M. pergandei* suggest that colonies may establish trails in directions away from interactions with neighbors (Ryti and Case, 1998). In a study of a related group forager, *Messor andrei*, foraging direction does not appear to be affected strongly by the distribution of food sources (Brown and Gordon, 2000). Experimental data suggested that foragers were more likely to return to locations where aggressive encounters with neighbors occurred in preceding days (Brown and Gordon, 2000). In contrast, previous studies suggest that *M. pergandei* colonies switch from group foraging along a column with rich, dense resources, to individual foraging when resource density is low (Rissing and Wheeler, 1976; Bernstein, 1975, reviewed in Plowes et al. (2013)). There is some evidence that incorporating information about the behavior of neighboring colonies is important, including that nearest neighbors tend to forage in opposite directions, especially when resources are low (Ryti and Case 1986, 1998). Our preliminary observations in *M. pergandei* suggest that after two colonies have an aggressive interaction (Fig. 1), one of the colonies is likely to refrain from long trails, and to have individual foraging <4 m from the nest, or to establish trails in directions away from the interaction (Ryti and Case, 1986).

The system which we model is novel for a number of reasons: first, it is derived from the behavioral repertoire of a species which shows highly dynamic spatio-temporal territories; second, our model describes the behavior of a group foraging social animal, and third, it is spatially explicit, incorporating neighbor interactions. We use our simulation model to test different foraging strategies, some of which might not be possible in ants or which have not been seen in ants. For instance, we explore how changing the nest density, nest distribution, or behavioral strategies can change the occurrence of aggressive encounters and foraging patterns at a population level. We can also study the spatial distribution of foraging from a different perspective: How intense is the resource exploitation regarding the total space occupied by a population of colonies, and what is the spatial distribution of exploitation? In addition, our simulations can run for long periods, providing more data than is possible in field observations.

2. Empirical data

2.1. Methods

We collected field data in Sonoran Desert Scrub, on Arizona State Trust land (32° 56'N, 111° 41'W), just north of Casa Grande, Arizona. A detailed habitat description can be found in Ode and Rissing (2002). Data used in this study was acquired from June 2008 through August 2009. Two dominant ant species are found at the site: *M. pergandei* and *P. rugosus*. Nests of *P. rugosus* were primarily located outside the study area.

In 2009, every colony of *M. pergandei* found in a 1 ha plot was mapped and marked, allowing us to calculate the density and distribution of nests (Fig. 2). *M. pergandei* is a monodomous species: the entire colony uses a single nest entrance. Monodomy was confirmed using behavioral tests where workers from