Interactions of foraging harvester ants (*Pogonomyrmex barbatus*)

Susan Holmes (Statistics, Stanford University), Bob Schafer (Stanford University)

Deborah Gordon (Biological Sciences, Stanford University)

Abstract:What regulates foraging activity in ant networks?

In a society without any central control, individuals decide which task to perform. We found that harvester ants (Pogonomyrmex barbatus) use the rate of brief antennal contacts in decisions whether to perform midden work, which is piling and sorting the colony refuse pile or midden. We have constructed what we call the interaction networks, each new interaction between two ants creates an edge in the interaction graph. Previous work has investigated how the use of encounter (6) rates affects the dynamics of task allocation. Physiological studies showed that ants of different task groups differ in cuticular hydrocarbons. Laboratory tests showed that cuticular hydrocarbons are used in nestmate recognition, suggesting that task-specific differences in odor are the cue assessed during antennal contact. Thus task-specific differences in hydrocarbons make it possible for ants to use rates of antennal contact in task decisions. We found that task-specific differences in cuticular hydrocarbons depend on external conditions, which explains how ants of different task groups come to differ in odor. Our work extends these results to field studies of foraging behavior and study of simulated ant colonies on which we have total control. Task allocation in social insects. Behavioral plasticity in social insects is especially interesting because colonies adjust to environmental change through the aggregated responses of individuals. Social insect colonies perform various tasks, such as foraging, nest work, and brood care. As environmental conditions and colony needs change, so do the numbers of workers engaged in each task. Task allocation is the process that adjusts the numbers of workers engaged in each task in a way appropriate to the current situation. Task allocation operates without central or hierarchical control. A basic question about social insects is how individuals, using local information about their surroundings and each other, in the aggregate produce the complex behavior of colonies. How does a worker decide what to do next? The process that relates individual decisions to local information determines how quickly and how accurately a colony can change its effort when conditions change.

Introduction

Social insect behavior can be studied at different levels of organization and complexity. Interactions among colonies and between colonies and the environment relay information that affects macroscopic trends in colony traits and behaviors. At a narrower perspective, investigations of individual colonies highlight behaviors such as reproduction, nest defense, and food collection, activities that are conducive to a consideration of each colony as its own entity. However, colony-level behaviors depend upon a smaller focus, that of the collective responses of all of the individual insects in a colony. Therefore, to understand the mechanisms of high-level behaviors to any degree of confidence, the behaviors of individual insects must be accounted for, at least on average. Following this strategy of understanding colony-level characteristics by delineating individual behaviors, the study conducted here has two broad goals: first, it describes and analyzes many aspects of one particular behavior, that of foraging in the red harvester ant Pogonomyrmex barbatus, in order to explain better the colony-level behavior of food acquisition. Second, it simulates individual foraging behavior in the context of a foraging network of ants, toward the aim of understanding the mechanisms by which the colony-level food acquisition emerges from individual foraging behavior. Foraging is only one of the jobs executed by worker ants of the species. Red harvester workers are allocated into groups of nest mates that collectively carry out one of four tasks:

- the underground chores of nest maintenance,
- the task of patrolling the nest mound and proximity around the nest,
- the job of creating and keeping the refuse piles, known as middens, that can be found near the nest entrance,
- foraging, or collecting food and retrieving it back to the nest (Gordon 1989(3)). Although each worker tends to perform the task that it performed the prior day, workers are able to switch from one task to another.

This dynamic task allocation follows strict rules, though, and not every transition between pairs of tasks is allowed; furthermore, some transitions are unidirectional. For example, once an ant has switched to foraging, it will not return back to engaging in any other task (3). Unlike various other species of ants, red harvester ant workers are all similar in size and body shape, so task transitions are not accompanied by differences in appearance.

Figure 1. A forager (one of three categories of workers) carrying a seed.

Observations

The field work was completed in August 2000-2002, in a 40-acre plot of land between Portal, Arizona, and Rodeo, New Mexico. Daytime soil temperatures exceeded 50^0C under direct sunlight. The daily procedure began at 5.30 am, and selecting a nest to follow for the length of the day. Nest selection was largely random, but only nests that promised extensive foraging for the day (measured by patroller activity and gathering at the nest entrance) were selected. Next, the nest was monitored while patrollers departed and returned. When the first foragers began to leave the nest, observations of individual workers began. A stopwatch was started as an ant left the nest, and, under the condition that it proved to be a forager, it was followed as it traveled to its foraging area. Small, colored flags were placed in the ground at significant locations, including the points at which the ant began searching for food, found food, gave up searching, or interacted with other ants. In the 2000 study ants were marked with paint, so individual's were followed precisely.

Figure 2. Ants interacting

Statistical Analysis

Data were analyzed using various statistical methods relevant to the questions posed. Foraging success rates (number of ants returning with food divided by total number of foragers) were taken directly from the observations, as was the mean number of interactions made by each forager while in the field. To determine the tendency of foragers to drift during their searches for food, the mean distance-from-nest (DFN) at search beginning was subtracted from the DFN at search completion, and this distance was divided by the amount of time spent searching. Significance of this drift was measured with a t-test. Search durations between groups of foragers were compared with a Wilcoxon two-sample test. Finally, the mean rate of interactions was extracted from the linear regression of data points on a graph of number of interactions versus foraging time, and confidence limits were found around the slope of the regression line (and therefore around the mean number of interactions per minute).

Simulation Study

The computer model of network foraging behavior was written as a script for Matlab. Each run of the script was designed to simulate a morning of foraging, beginning with the first foragers leaving the nest and ending after 18,000 seconds (5 hours) of simulated time had elapsed. Only foragers were included in the simulation. In the simulation, each forager leaves the nest, travels for a set distance on a foraging trail, begins its search, finds food or gives up, returns to the trail, and returns to the nest. Interactions between foragers during their searches were recorded, as were the numbers food items collected. The foraging area was a simulated 40m by 40m square, with the nest at (20m,20m) and reflecting boundaries at the edges of the square.

The parameters used in this model fall under three categories: environmental, colony-level, and individual (Table 2). At the level of the environment, these parameters include temperature, number and proximity of neighboring P. barbatus colonies, number of food items scattered through the foraging area. Temperature follows a sine curve set with maximum and minimum determined by data collected for averages in the month of August in Rodeo, New Mexico. All simulations were run with one neighboring colony, centered at (10m,10m) in the foraging area. The number of food items ranged from 30,000 to 100,000 in the $1600m^2$ foraging area, corresponding to food densities of approximately 20 to 60 seeds per square meter. This number is significantly smaller than estimates of standing seed crops made by Price and Reichman (1987) to compensate for the limited depth at which a harvester ant can extract a seed: only those seeds on or very near the surface of the ground can be located and collected. Food is scattered randomly over much of the foraging area, but is negatively weighted around the focal nest and neighboring nest. This distribution results from the likelihood that, on any randomly selected summer day, the area closest to harvester ant nests will be most heavily searched.

Type of parameter	Name	Default setting
Environmental	Temperature	Sine curve, 17-62° C ground temp
	Number of neighbors	1
	Proximity of neighbors	14.14m
	Food items	30,000-100,000
Colony-level	Number of foraging trails	2
	Direction of trails	3/4, 3/2
	Length of trails	4m
Individual	Step length	1.526 cm/s
	Radius of detection	0.5 cm
	Time until give up search	200 s
	Standard dev of turning angle	0.5 radians
	Drift	0.01% per step
	Effects of interactions	Change give up time to 1200 s

Table 1: A list of the parameters used in the computer simulation, and the default settings used unless otherwise stated.

The next group of parameters is the colony-level variables. These include the number, directions and lengths of foraging trails in use, and the number of ants that are available to make foraging trips. In all of the simulations run here, two foraging trails are used, departing at different angles from the nest with equal average numbers of ants departing down each of the trails. Both trails are 400 times the step-length in length, and extend at a rate of 5 times the step length per degree Celsius throughout the day, to simulate roughly the observed extension of trail lengths over the course of the day in the field (Gordon 1995 (4)). The number of foragers available in each simulated colony was 1000, which approximates the number of active foragers in a typical two-year-old colony (Adler & Gordon 2003).

The final group of parameters describes individual forager behavior, and includes variables for step length, radius of detection of food and other ants, the number of steps an ant will take while searching before quitting, the standard deviation of turning angle, drift away from the nest, and the effects of interactions, including the reencounter avoidance response and the extent and valence of all resulting behavioral changes. The step length is defined as the distance traveled in one second, and is temperature-dependent according to the equation described by Morehead and Feener (1998). The step length during the coldest part of the morning is approximately 1.5 cm/second, increasing to about four times this length at about 11:00 in the morning.

The radius of detection is approximated at 0.5 cm from field observations. When a seed or nest mate is within this distance from the forager, it will either discover the seed, or interact with the other worker. The number of steps an ant will take while searching before quitting is determined by a normal distribution of standard deviation 40, centered around a mean of 200 steps. The standard deviation of turning angle describes the randomness of an ant's walk: a number is chosen at random from a normal distribution set around zero, and this number is added to the prior step's direction (in radians). When the variance of the normal distribution is large, the direction of each step may change dramatically. A value of 5 results virtually in a random walk; here, a value of 0.5 is used, based on work by Adler and Gordon (1992) (2) that evaluated foraging strategies based on the interaction and the number of ants in a network. The drift parameter determines the rate at which a forager will drift in the direction away from the nest while it is foraging. In the field, drift is approximately 0.25 cm/second away from the nest. To simulate this, the direction of each step is slightly skewed.

The last worker-level parameter describes the manner in which individual foraging behavior changes as a result of forager-forager interactions. Searching foragers that have made at least one interaction are willing to search for a greater period of time before giving up, as determined by the field segment of this study. In this simulation, the time before quitting is increased to 1200 steps, with a standard deviation of 350 steps. Besides the environmental, colony-level, and individual parameters, this simulation tested four different methods used to determine the rate of departure of foragers from the nest. Three of the methods use a departure parameter, λ, that represents the mean number of ants leaving the nest during any given second, as determined by a Poisson random number generator using mean λ. During the simulation, λ is always capped at 1.5 ants/second, an approximation of the physical bottleneck of foragers leaving the nest entrance. All methods have a static departure rate of 0.5 ants/second for the first 800 seconds, which approximates the minimum time required for an ant to traverse the foraging trail, immediately find a food item, and return to the nest.

Simulation Summary

This interaction rate equates to one every 5.96 minutes.

There is a positive correlation between amount of time searched and distance drifted away from the nest.

Foragers tend to direct their searches away from the nest, terminating their searches farther from the nest than they begin searching. This drift is independent of the number of interactions made by that forager.

Mean search duration	Successful	Unsuccessful
Interactions	1226s, n=11	1240s, n=5
No interactions	148s, n=7	112s, n=3

Table 2: Search times depend heavily on whether interactions have occurred, not on the success of the foraging run.

Figure 3 : Forager ant carrying a seed back to the nest.

Conclusions and perspectives

The comparison of the simulation and the observational studies shows a good fit between the model and the data. However as the number of parameters that are input in the model is large, there remains problems regarding the identifiability of the simulation that have to be solved before we can proceed further with the comparison.

We are now studying the statistical properties of the ant network parameters, number of connected components and particularly frequent subgraphs (9) using algorithms such as those in (7) with the statistical package R ((1)).

This work was funded in part by an interdisciplinary grant from Bio-X at Stanford University

REFERENCES

Ross Ihaka and Robert Gentleman, (1996), R: A Language for Data Analysis and Graphics, *Journal of Computational and Graphical Statistics*, 5:299–314. http://cran.r-project.org/

Adler, F. R. and D. M. Gordon. (1992) Information collection and spread by networks of patrolling ants. *American Naturalist*, 40:373-400.

Gordon, D. M. (1989) Dynamics of task switching in harvester ants. *Animal Behaviour*, 38: 194-204.

Gordon, D. M. (1995) The expandable network of ant exploration. *Animal Behaviour*, 50:995-1007.

Gordon, D. M. 1999. *Ants at Work*. Free Press, Simon and Schuster, NY, and 2000 (paperback) Norton.

Gordon, D. M. and N. Mehdiabadi. 1999. Encounter rates and task allocation in harvester ants. *Behavioral Ecology Sociobiology* 45:370-77.

Holmes, S. 2001. Statistics in Computational Genetics, http://www-stat.stanford.edu/~susan/courses/s366/.

Holmes, S. , Schafer B. and Gordon, D. Interaction networks in ants , a comparison of obervation and simulation studies. (in preparation).

Shen-Orr, S., Milo, R. , Mangan S. & Alon, U. Network motifs in the transcriptional regulation network of Escherichia coli. Nature Genetics, 31:64-68 (2002).

Wagner, D., Tissot, M. and D. M. Gordon. (2001) Task-related environment alters the cuticular hydrocarbon composition of harvester ants. *J. Chemical Ecology*, 27:1805-1819.

This poster was prepared with Brian Wolven's Poster LaTeX macros v2.1.