BIOLOGY AND MODELING OF SELF-ORGANIZATION
IN THE NEW WORLD ARMY ANT
ECITON BURCHELLII

by

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ABSTRACT

The study of self-organization seeks to understand how complex system-level patterns emerge from the behavior of simple components within living systems. A significant challenge for such research is the lack of easy-to-use tools to quantify behaviors at the individual and system level. This work presents an effort to develop some of these tools and apply them to understanding the rules underlying self-organized swarming behavior in the New World army ant *Eciton burchellii*.

*E. burchellii* swarms exhibit self-organization in that they collectively perform computationally complex tasks without centralized control and with access to only local information. To swarm successfully *E. burchellii* must spatially coordinate up to 200,000 nearly blind individuals of multiple castes in the face of changing biotic and abiotic factors. Large swarms can raid over an area larger than 2,000 m² per day, processing and retrieving 30,000 or more prey. Swarms are robust to drastic changes in size and huge variations in substrate. Individuals have no means to measure overall spatial distribution or foraging success within different parts of the swarm. Self-organization provides evolution a mechanism by which selection on such simple individual behaviors can generate complex system-level patterns.

In this thesis I examine the individual behavioral rules through which foraging swarms of *E. burchellii* are organized. To accomplish this, we measured the body positions of more than 30,000 ants in video of swarms from Costa Rica. From these data we generated a map approximating the pheromone landscape experienced by the ants. This landscape was matched with ant path data enabling us to quantitatively measure how *E. burchellii* army ants modify their turn angle and velocity in response to pheromone. Our measurements also provided evidence that ants of different lengths perform different functions in the swarm. These results were integrated into an individual-based computer model of army ant swarming that was tested against the video data.

Our data and model results suggest that simple rules governing how velocity and turn angle change in response to variations in pheromone concentration and local ant density are enough to qualitatively reproduce many of the complex swarming behaviors observed in the field.
There is a way between voice and presence
where information flows.
In disciplined silence it opens.
With wandering talk it closes.
- Rumi (tr. C. Barks)

This work is dedicated to my son Leo Holden Brown (b. Sept. 1, 2006). May you escape into adulthood with your sense of wonder intact, may you forgive us for the state in which we leave you the world, and may you delight in the marvelous things we have discovered.
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CHAPTER 1

WHY STUDY COMPLEX SYSTEMS AND SELF-ORGANIZATION?

Overview

A significant shortcoming in the scientific understanding of evolution is the lack of a mechanistic explanation for how high-level complex patterns can evolve from simple components. In order for natural selection to act in the process of evolution, every step in the path from simple to complex structures must be adaptive. While a detailed picture has been drawn of how complex organs such as the eye have evolved (Dawkins 1997), systems such as the immune system or the human brain exhibit levels of complexity that are hard for many to imagine appearing through a linear, evolutionary path. Indeed many, if not all of the most interesting phenomena in biology are characterized by nonlinear or “emergent” processes. These are processes in which the exact path by which scaling from individual system parts – such as species or neurons – to system-level processes like ecosystem dynamics or human consciousness is not clear. As a result, science, particularly ecology, has had great difficulty in developing theories about these types of systems that have much predictive power.

The lack of a mechanistic explanation for how high-level complex patterns can evolve through natural selection on simple units is a significant drawback in the scientific understanding of evolution. This problem is particularly concerning because of the accelerating impacts humans are having on ecosystems globally (Hassan et al. 2005; Reid et al. 2005). Without a robust ability to predict how changes will affect ecosystem function and stability, scientists lack the tool to advise policy makers effectively (Solé and Bascompte 2006). The lack of a mechanistic explanation for the evolution of high-level, complex patterns is also problematic for political and educational reasons because this gap in our understanding has been seized on by pseudoscientific creationist organizations who argue the complexity we see in the world is just too “complex” to be explained through evolution (e.g., Behe 1996; Campbell and Meyer 2004). Most scientists write creationist arguments off as fallacious, but these views hold increasingly strong sway with a public who understand little of evolution and even less of complexity science (Coyle 2005; Gross 2006; Shulevitz 2006). While there are social and political forces behind this trend, the problem is aggravated by lack of a coherent theoretical framework for examining these questions in a scientifically rigorous manner.

Complexity

The newly developing field of “complexity science” seeks to understand, often through multidisciplinary research, how natural systems achieve the high-level complexity we observe (for a good introduction to complex systems research, see Gallagher and Appenzeller 1999b). In recent years, there has been an explosion of scientific and popular interest in the study of complex systems, (e.g., Gallagher and
Appenzeller; Holland 2000; Lewin 2000; Camazine 2001; Strogatz 2003). Although there are many definitions of complexity and complex systems, for this work, we will define it as a process or system whose properties cannot be completely explained through a simple description of its component parts (Gallagher and Appenzeller 1999a). A key component of complex systems is that the translation of behaviors from individual components to system-level properties is nonlinear and therefore not directly predictable from a description of its parts (Camazine 2001). Complex systems can be structurally quite simple – these systems are “complex” because of the complexity of system behavior, which is often generated through “simple” parts. An additional property of complex systems is that small changes in early conditions or behavioral rules often result in widely divergent or unpredictable behaviors (Camazine 2001). This observation is significant because it provides a potential mechanism for evolving systems to explore the fitness landscape in less linear ways than are normally considered possible. This has significant implications for our understanding of how evolution works.

**Self-organization**

A process fundamental to the study of complex systems is the idea of self-organization. Self-organization can be defined as the process by which the behavior of a group of interacting agents or components generates complex system-level behaviors which are not directly predictable from knowledge of the behaviors of individual components (Camazine 2001). Although this sounds similar to the definition of complexity, the important difference is that self-organization is a specific process found in living systems, whereas “complexity” describes the behavior resulting from these systems. The study of self-organization seeks, in part, to describe functional mechanisms by which natural selection on simple rule-sets and behaviors can generate the higher-order complexity observed in living systems (Kauffman 1993; Camazine 2001).

Investigation of complex systems and self-organization, while somewhat new to the biological sciences, has been a topic of much research in physics and chemistry (e.g., Schrödinger 1946; Nicolis and Prigogine 1977). In those fields, a combination of empirical research and mathematical and computational modeling has provided researchers with a set of descriptive tools with significant predictive power. This approach has been much slower in coming to the biological sciences. In biology, self-organization, as a concept, is often dismissed because it is not perceived as a concrete set of mechanisms with much descriptive power. However, this perceived problem stems not from a lack of utility of self-organization as a concept but from the real difficulty in describing phenomena that are highly nonlinear. Science generally proceeds through the production of positive results. Systems that may be interesting, but are largely intractable, get less attention because they are so difficult to work with. However, the processes of life are massively nonlinear by definition and, if we are to truly understand how these systems work, an essential first step is the development of a conceptual framework that acknowledges the importance of emergent phenomena. Rigorous clarification of the mechanisms underlying self-organization can help define this framework.
As human impact on the environment increases, resource managers are being required to develop management plans for a wide range of natural systems (e.g., Chopra et al. 2005). To do so effectively requires we understand the determinants of ecosystem structure and stability. If it is true, in general, that ecosystem-level processes are highly nonlinear (Solé and Bascompte 2006), management efforts that fail to acknowledge this fact risk failure. At least, there is the danger we may find the complexity of the ecosystems we manage has been reduced to match the simplicity of our models (Pimm 1992; Langston 1996; Taylor 1999).

Prior to Darwin’s work (Darwin 1859), the concept of evolutionary modification of traits over time was not even included in the realm of scientific discourse. Similarly, until Mendel’s research (Mendel 1865), the scientific community had no framework for understanding how traits were passed down from parent to offspring. It took decades of detailed work by Darwin, Mendel and others, to generate datasets permitting the development of the theories of evolution and inheritance.

The study of self-organization suffers from a similar problem. Quantitative descriptions of nonlinear phenomena require a significant amount of data. In addition, the mathematical and computational tools needed to process and model such datasets present huge barriers to entry in this field. Simply put, a field that requires advanced skills in biology, computer programming, mathematics and statistical analysis is not an area of research that is accessible to the general scientific community. Consequently it has proved difficult to develop a set of practical tools and theories that permit wider application of complexity science for general biology. However, recent progressions in technology provide us the necessary computational tools to examine complex, nonlinear processes in living systems in a quantitative way. Indeed, the work of this thesis could not have been undertaken even a decade ago because sufficient desktop computer processing power did not exist. Likewise, in a few years, when automated video tracking systems are readily available, a more detailed version of the work in this thesis could be accomplished in a few months rather than over multiple years.

When enough quantitative research on self-organized phenomena has taken place – combining extensive real-world data sets with detailed mathematical and computer models – we will find that self-organization is not a vague idea, but a discernable set of mechanisms with considerable explanatory power. For this to take place, we must have a toolbox of well-described model systems, easy to use data collection tools and agent-based modeling programs. The development of these types of tools will empower us to examine nonlinear biological phenomena in the same way that tools like PCR and model organisms such as *C. elegans* and *Drosophila* have accelerated progress in molecular biology.

What is not self-organized?

In order to understand the significance of self-organization, it is worth reviewing what types of complex biological processes are not self-organized. A few commonly
occurring mechanisms that are not self-organized are templates and recipes and leaders or pacemakers.

Templates and blueprints: Perhaps the best known template in living systems is DNA and RNA. Although many cellular processes are self-organized, a fundamental part of all cellular machinery are the templates of DNA and RNA. An immense level of complexity emerges from the cellular architecture associated with these molecules.

Although many organisms build complex living structures with self-organized processes (e.g., Bonabeau et al. 1998b; Camazine 2001) some spiders, bees and solitary wasps have been shown to build their webs or nests using a genetically coded blueprint (Camazine 2001). Weaver birds have been shown to use the shape of their own bodies as when building their nests (Camazine 2001).

Pacemakers: Pacemakers are important in many biological processes. The best known example is probably the pacemaker cells that drive the mammalian heart (Lewis et al. 1910). Pacemakers also play a prominent role throughout the multicellular aggregation process in the slime-mold Dictyostelium discoideum. Multicellular aggregation in Dictyostelium is, by and large, a self-organized process, yet the pacemaker cells drive the formation of the aggregation centers required for individual cells to collect to form the slug (Kessin 2001). After the slug has formed, they drive slug locomotion by rhythmically releasing cAMP (Kessin 2001). The role of pacemakers in Dictyostelium aggregation is interesting because it provides a clear example of a process that, while overall, is self-organized (Camazine 2001), requires a mechanism that is not self-organized to progress correctly. This suggests that there are certain types of functional and organizational problems that cannot be solved through self-organization.

What is perhaps most notable about non self-organized processes in living systems is that there are so few of them. Self-organization is ubiquitous in living systems because it provides an important mechanism for the solution of a wide range of evolutionary problems. The implications of this will be examined in greater detail in Chapter 5.

Other aspects of complex systems

A number of additional lines of inquiry related to self-organization have informed the work in this thesis. Primary among them is an interest in understanding how the architecture of a network of interacting components influences the complexity of behavioral responses or states available to that system. A wide body of literature ranging from neuroscience (Johansen-Berg et al.; Claus and Simon 2000; Young and Scannell 2000; Bond 2001), to entomology (Adler and Gordon 1992; Gordon et al. 1992; Pacala et al. 1996) to genetics (Kauffman 1993; Salazar-Ciudad et al. 2000), to internet routing and networking (Barabási 2002; Valverde and Solé 2004; Valverde 2005) indicates that in a wide range of systems, system function is highly related to system architecture. Research in all these fields suggests that internal connectivity and interaction rates between nodes
within the system play a large role in determining system efficiency and the rate at which the systems can process and respond to new information.

Research in this area using cellular automata models has demonstrated that information processing and system stability are both highly dependent on the number of nodes within a system and the number of other nodes to which each system member is connected. Langton’s work with cellular automata models (Langton 1990) suggests that the emergence of system stability and peak levels of computation take place in systems that are poised on the edge between highly chaotic and fixed states. Kauffman (1991; 1993) examined the role that network connectivity plays in this process. He found that cellular automata systems with an optimal degree of inter-nodal connectivity can spontaneously exhibit highly organized states. Kauffman has presented a reasonable case that evolving gene networks undergo similar transitions (Kauffman 1993). Additional work extending Kauffman’s original models (Kauffman and Levin 1987; Bilke and Sjönnneson 2001; Solé et al. 2003; Mochizuki 2005; Solé and Bascompte 2006) indicates that the emergent properties of such complex adaptive networks enables them to rapidly explore a wide range of novel behaviors or patterns. This is an important observation because it provides a mechanism by which novel types of organization in living systems can evolve much more quickly than is usually supposed (Solé et al. 2003). However the implications of such results for our understanding of the evolution are only starting to be explored (Solé and Bascompte 2006).

An additional line of inquiry has applicability for understanding how complex systems evolve. It has been well documented in neurobiological research that quality of signal processing in organisms is to a large degree dependent on the size of the neural network devoted to processing the signal (Bullock 1986; Suga 1990). For instance, in bats who “see” primarily with sound, some 30% of the primary audio cortex is devoted to analysis of a few kilohertz of the audio frequency spectrum (Suga 1989; Suga 1990). The implication is that in order for bats to achieve the level of audio acuity they require, they must devote a neural network of a certain complexity to signal processing. In contrast, a far smaller portion of the human brain processes sound, but because visual input is so important to humans, our visual cortex is quite large (Drasdo 1977). Such observations also hint that there may be a fundamental relationship between how well a system can process information, and its internal interconnectivity and the rate of information transfer within the system.

Although it is far less well understood, a similar tradeoff has been observed in ants. Work by Deborah Gordon and others (Gordon et al. 1993; Gordon 1994; Pacala et al. 1996) has shown that colonies of Pogonomyrmex workers regulate contact rate as colony size changes. A model by Adler and Gordon (1992) found that the movement of foraging information within a harvester ant colony is highly dependent on colony size and path topology. Their results suggest that there may be nonbiotic constraints on colony size due to network architecture created by information sharing between ants as they collectively forage. It remains to be seen if general conclusions can be drawn from such divergent systems. However, advances in the emerging field of “network science”
suggest that this may be a fruitful line of inquiry (Barabási 2002; for an overview of this topic).

**Study system**

As discussed earlier, an important first step in extending our understanding of complex systems and self-organization is the development of toolsets and well-described model systems to facilitate such research. Social insects are an ideal model system for this task for a number of reasons. First, due to their unique social structure, social insects blur the line between individual and system. Processes such as collective foraging emerge from the behavior of individuals, yet because individuals are sterile, their effectiveness is ultimately measured at the group level in terms of colony fitness. Despite their relatively simple neural capacities, social insects display an astonishing range of individual and collective behaviors (Hölldobler and Wilson 1990). Social insects are also ideal for modeling because both individual behaviors such as foraging choices and colony behaviors such as collective foraging success and colony fitness can be directly measured. The result is that one can create models of individuals and then compare the model output of their collective actions with real measurements of colony behavior. Finally, social insects demonstrate self-organized behaviors in that many processes which determine colony fitness such as foraging and nest building result from the actions of individuals with limited or no global knowledge (see Deneubourg et al. 1989; Goss et al. 1990; Beckers et al. 1992; Bonabeau et al. 1997; Bonabeau 1998; Camazine 2001 and others).

This thesis represents a small exploration of how one, incredibly complex social insect, the New World army ant *Eciton burchellii* manages to accomplish amazing feats of organization without a centralized control system or director. Of all the social insects, one could argue that swarm raiding army ants exhibit some of the most visually impressive displays of self-organization. African army ant colonies (*Dorylus* spp.) can reaches sizes of 20 million individuals (Schneirla 1971). In the New World, *Eciton burchellii* is probably the most conspicuous army ant with colony sizes reaching 600,000 individuals (Schneirla 1971) and diurnal, surface raids of 200,000 or more individuals (Franks 1982a). *E. burchellii* has a five week life cycle in which it alternates between 2 weeks of daily raids and nightly emigrations and then 3 weeks in which it is stationary and raids less frequently. In the stationary phase, the queen lays some 50,000 eggs in less than 7 days (Franks 1985). When the eggs hatch, the increased food demands of the new larvae induce the ants to begin their nomadic phase and the cycle starts again (Schneirla 1971).

The organizational complexity of army ant swarm behavior is immediately striking to any who observe them in the field. As R. Wroughton (1892) noted more than 100 years ago, “The notion irresistibly forced on anyone, watching these maneuvers, is that they are either the result of pre-concerted arrangement, or are carried out by word of command.” Yet amazingly, swarming behavior is not coordinated by any supervising
force but emerges from collective interactions of tens of thousands of ants who have no means to globally assess the pattern they are creating.

The goal of the research in this thesis is as follows:

1) To examine a particular self-organized process, that of swarming in *E. burchellii*, in quantitative detail.

2) To apply these data to parameterize an individual based model of swarming in *E. burchellii*. The model allows us to test the accuracy of hypotheses generated through our quantitative analysis as well as to make predictions that can be tested in the field.

3) To develop a set of tools for analyzing swarming behavior in *E. burchellii* and self-organized behaviors in ants in general, that make a small contribution to the toolbox available for researchers in self-organization and complexity science.
CHAPTER 2

SELF-ORGANIZED PROCESSES IN ECITON BURCHELLII ARMY ANT SWARMS. SIMPLE RULES FOR SOLVING COMPLEX PROBLEMS

Abstract

One of the primary goals of research into self-organized phenomena is to describe how simple behavioral decisions at the individual level scale to emergent group-level processes. We present the first quantitative examination of the individual behavioral rules through which Eciton burchellii army ants organize their swarms. To swarm successfully the New World army ant E. burchellii must spatially coordinate tens of thousands of nearly blind individuals of multiple castes in the face of changing biotic and abiotic conditions. Individuals have no means to measure overall spatial distribution of ants or foraging success within different parts of the swarm. Foraging swarms of E. burchellii are self-organized in that they collectively perform computationally complex tasks without centralized control and with access to only local information.

We measured the body positions of more than 30,000 ants in digital video of E. burchellii swarms from Costa Rica. From these data, we generated a map approximating the changing pheromone landscape experienced by the ants over time. This approximate pheromone landscape was matched with ant path data enabling us to quantitatively measure how E. burchellii army ants modify their turn angle and speed in response to pheromone. Our results suggest that E. burchellii swarms are organized using only simple rules governing how speed and turn angle change in response to variations in pheromone concentration and local ant density. We also found that ants of different lengths perform different functions in the swarm.

Introduction

Social insect colonies are an ideal model for investigating the role that self-organization plays in the evolution and optimization of living systems. Self-organization is generally defined as the process by which the behavior of a group of interacting agents or components generates complex system-level behaviors which are not directly predictable from knowledge of the behaviors of individual elements of the system (Camazine 2001). In self-organized systems, individuals have little or no knowledge of the global pattern they are creating. Instead, system-level behavioral processes emerge as a result of lower level interactions. Self-organization provides a specific mechanism for natural selection to generate higher-order processes by selection on simple individual behaviors (Kauffman 1993; Camazine 2001). Social insects demonstrate self-organized behavior in that many processes that determine colony fitness such as foraging and nest building result from the actions of individuals with limited or no global knowledge (Deneubourg et al. 1989; Goss et al. 1990; Beckers et al. 1992; Bonabeau 1998).
We have investigated the individual behavioral rules that organize the complex foraging swarms of the New World army ant *Eciton burchellii*. Self-organization in army ant swarms provides a mechanism by which changes in simple individual behaviors such as speed or turn angle, in response to variations in pheromone concentration or local ant density, can, when summed over the whole swarm, generate effective group foraging decisions. To swarm successfully the ants must coordinate as many as 200,000 nearly blind individuals (Schneirla 1971) of multiple castes (Franks 1985) in the face of fluctuating and unpredictable biotic and abiotic factors.

Large swarms can forage over an area of 1,500 square meters in a 12–14 hour day (Schneirla 1971; Franks 1982a; Swartz 1997), capturing, processing and retrieving more than 30,000 prey items (Franks 1982b). Swarms typically move forward at about 14 - 18 meters per hour (Table 1) while maintaining a cohesive swarm front as wide as 15 meters (Schneirla 1940; Swartz 1997). *E. burchellii* swarms are robust to drastic changes in size and can function with a few thousand or a few hundred thousand individuals (T. Brown, unpublished data). The substrate on which they forage can vary from clear ground to highly three-dimensional tree-fall gaps hundreds of meters square and 5 meters or more deep. *E. burchellii* forages without a centralized control system. The ants have access to only the information available from ant-ant interactions and local pheromone concentrations and individuals have no means to measure overall spatial distribution or foraging success in other parts of the swarm.

*E. burchellii* are swarm raiders. In swarm raiding army ants, capture success depends on the ants maintaining a relatively high density of ants over a large area so that any prey flushed by the swarm can find no clear escape route (T. Brown, unpublished data). This type of foraging contrasts with that of column raiding army ants such as
Table 1 Summary of measured ant running speeds and swarm front velocities.

### a  Individuals in swarms, clip 1, current work.

<table>
<thead>
<tr>
<th>Mean speed in cm / sec (range)</th>
<th>St. Dev.</th>
<th>Sample Size</th>
<th>Measurement type</th>
<th>Swarm State</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.7 (0 – 19.8)</td>
<td>2.2</td>
<td>160 Ants</td>
<td>25,056 samples</td>
<td>All ants</td>
<td>Nomadic</td>
</tr>
<tr>
<td>3.9 (0 – 18.3)</td>
<td>2.4</td>
<td>55 Ants</td>
<td>13,279 samples</td>
<td>Early pioneer ants [before frame 3000, Fig. 1, 2 (A)]</td>
<td>Topoff et al, 1972</td>
</tr>
<tr>
<td>3.6 (0 – 19.8)</td>
<td>2.1</td>
<td>42 Ants</td>
<td>5,071 samples</td>
<td>Ants in “eddy line area [after frame 3000, before 4400, Fig. 1,2 (B)]</td>
<td>Topoff et al, 1973</td>
</tr>
<tr>
<td>3.3 (0 – 10.8)</td>
<td>1.7</td>
<td>68 Ants</td>
<td>6,701 samples</td>
<td>Ants in main swarm [after frame 4400, Fig. 1,2 (C)]</td>
<td>Topoff et al, 1973</td>
</tr>
</tbody>
</table>

### b  Individuals on Trails.

<table>
<thead>
<tr>
<th>Mean speed (cm / sec)</th>
<th>St. Dev. (cm / sec)</th>
<th>Sample Size in Ants</th>
<th>Measurement type</th>
<th>Swarm State</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>9.4</td>
<td>1.8</td>
<td>207</td>
<td>Circular mill w/trail extract</td>
<td>Mixed</td>
<td>Franks, 1985</td>
</tr>
<tr>
<td>7.9</td>
<td>1.9</td>
<td>127</td>
<td>Circular mill w/trail extract</td>
<td>Mixed</td>
<td>Franks, 1985</td>
</tr>
<tr>
<td>5.1-11.5</td>
<td>12</td>
<td>62</td>
<td>Un-laden ants on trails</td>
<td>NR</td>
<td>Franks, 1985</td>
</tr>
<tr>
<td>8.4</td>
<td>1.5</td>
<td>50</td>
<td>Teams with prey, on trails</td>
<td>NR</td>
<td>Franks, 1985</td>
</tr>
<tr>
<td>7.96</td>
<td>1.2</td>
<td>50</td>
<td>Plastic circular mill</td>
<td>NR</td>
<td>Franks et al, 1991</td>
</tr>
<tr>
<td>3.5</td>
<td>NR</td>
<td>Groups of 40 workers on 180 min old trail</td>
<td>Plastic circular mill</td>
<td>NR</td>
<td>Franks et al, 1991</td>
</tr>
<tr>
<td>5.8</td>
<td>0.7</td>
<td>12</td>
<td>Plastic circular mill</td>
<td>NR</td>
<td>Franks et al, 1991</td>
</tr>
<tr>
<td>6.5</td>
<td>0.6</td>
<td>50</td>
<td>Plastic circular mill</td>
<td>NR</td>
<td>Franks et al, 1991</td>
</tr>
<tr>
<td>6 – 11</td>
<td>NR</td>
<td>Trails; Paper circular mill with gland extract</td>
<td>NR</td>
<td>Billen &amp; Gobin, 1996</td>
<td></td>
</tr>
<tr>
<td>13 (model max vel.)</td>
<td>NR</td>
<td>NR</td>
<td>Ants on trails</td>
<td>NR</td>
<td>Couzin &amp; Franks, 2002</td>
</tr>
<tr>
<td>5.1 – 12.5 cm / sec</td>
<td>NR</td>
<td>50 ants, 3 colonies</td>
<td>Single ants with prey on controlled substrate</td>
<td>NR</td>
<td>Powell &amp; Franks, 2005</td>
</tr>
</tbody>
</table>

### c  Swarm front speed.

<table>
<thead>
<tr>
<th>Mean speed (m / hr)</th>
<th>Mean Speed (cm / sec)</th>
<th>St. Dev. (m / hr)</th>
<th>Sample Size (swarms)</th>
<th>Swarm State</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>14.8</td>
<td>0.42</td>
<td>NR</td>
<td>113</td>
<td>NR</td>
<td>Willis, 1967</td>
</tr>
<tr>
<td>17.61</td>
<td>0.48</td>
<td>0.11</td>
<td>9</td>
<td>NR</td>
<td>Swartz, 1997</td>
</tr>
<tr>
<td>NA</td>
<td>2.10 – 2.19</td>
<td>NA</td>
<td>2</td>
<td>Nomadic</td>
<td>Chapter 3</td>
</tr>
</tbody>
</table>

* NR = Not reported
** NA = Not applicable
*Eciton hamatum.* *E. hamatum* specializes on rare, high-quality prey resources, primarily other *Hymenoptera* nests (Chadab and Rettenmeyer 1975). In column raiding species, foraging success depends on effectively mobilizing highly coordinated, smaller groups of ants to swiftly attack their prey. Like most New World army ants, much of *E. burchelli* prey is small social insects and their eggs and larvae. (Franks 1982b; Franks and Bossert 1983; Otis et al. 1986; Powell and Franks 2005). However, *E. burchelli* are unique among the *Eciton* in that about 50% of their diet consists of large nonsocial arthropods such as cockroaches, spiders and katydids (Powell and Franks 2005). These large prey items add an additional level of complexity to the spatial coordination of foraging. To capture and subdue such large prey, the ants must maintain high local densities of ants in as much of the swarm front as possible. In addition, once captured, large prey items must be cut into pieces small enough to be transported to the nest, which can be 100 m or more away. Prey processing can take hours for each large prey item (Wrege et al. 2005). The above-noted differences in prey distribution and capture strategy have important implications for how *E. burchelli* organizes its swarms (Deneubourg et al. 1989). For instance, Powell and Franks (2005) recently showed that the evolution of a “submajor” caste in *E. burchelli* was most likely driven by evolutionary pressures associated with the processing and transport of large non-*Hymenoptera* prey items.

In 1940, T.C. Schneirla laid out what remains the definitive, qualitative description of the organization of *E. burchelli* foraging swarms. We summarize the most relevant points here (and see Fig. 1). In the densest part of the swarm, ants experience
A typical swarm raid with detail of swarm front. Letters denote different parts of the raid. A Area in front of swarm. Low ant density and little or no pheromone present. B "Eddy line" area where returning pioneers bump into outgoing ants (see discussion). C Main swarm, area of highest density. D Rear of swarm, beginning of the "fan." E Back of fan where trails coalesce into one main trunk trail. Image based on Rettenmeyer, 1963 (used with permission).

high levels of pheromone and are in a high level of excitation (Fig. 1 C). By chance, some of these ants run forward past their nest-mates and out into areas in front of the swarm where there is little or no pheromone on the ground and there are few or no other ants (Fig. 1 A). Schneirla called these single ants that lead the swarm “pioneers.” He hypothesized that the pioneer ants were not a unique caste but “any worker[s]” that happened to run forward out of the main swarm. As soon as an ant finds itself in an area with low ant density and low pheromone levels, its speed slows rapidly and its probability of turning increases. Turning frequently, the ant moves hesitantly forward a few centimeters to a meter while marking the substrate with pheromone. Soon, the high turn rate induced by lack of pheromone causes the ant’s path to loop back on itself and it runs back into the main part of the swarm. As the ant returns to the swarm front, it bumps into higher densities of ants that are running outwards and quickly turns around (Fig. 1 B). This collision of ants has a slight disruptive and slowing effect on the front of the swarm, but as long as the numbers and outward pressure of the ants in the swarm front is sufficient, returning ants will turn around and begin to run with the swarm again. As other ants pass these returning pioneers and run out ahead of the swarm, they become pioneers themselves. This process repeats, strengthening and extending the first faint trails and the densest part of the swarm moves onto the newly marked ground.

E. burchellii swarms have a characteristic tree-like shape with a dense flat front that is typically a few meters deep (Fig. 1 C). Behind the main swarm is a progressively less dense “fan” area of many interlinked trails stretching back 5 or more meters (Fig. 1 D, E). Behind the fan, these trails thin and become more centralized until there is typically a single, densely traveled trunk trail, which leads back to the bivouac. Because all trails from the swarm front feed into the trunk trail, ants can easily return to the bivouac. Likewise, ants running out along the main trail from the bivouac encounter a series of branching intersections leading to all parts of the swarm.

Schneirla hypothesized that the characteristic flat front and tree-like shape of E. burchellii swarms is due to the interaction between the “frontal barrier” caused by the lack of pheromone in areas not yet explored and the “basal pressure” of new ants arriving from the back of the swarm. The flattening pressure of the low-pheromone areas is intensified by disordering effects of returning pioneers bumping into outgoing ants prior to changing direction.

Schneirla’s detailed analysis of swarming behavior (Schneirla 1940; Schneirla 1971 and others) suggests that observed swarming patterns are primarily a result of the reactions of individual ants to differing pheromone levels and local density. Secondary factors influencing swarm behavior and pattern fall into three broad categories. 1) Local
factors such as variations in substrate, prey encounters; 2) global abiotic factors such as temperature, precipitation, time of day; and 3) colony level factors such as colony status (e.g., whether a colony is nomadic or stationary). More recent work has found that there is size-based behavioral differentiation in *E. burchellii* for prey retrieval (Franks 1985; Franks 1986; Franks et al. 1999) and that trails form preferentially on substrates along which it is easier to travel (Powell and Franks 2005). Swartz (1997) found a negative correlation between swarm width and intensity (number of ants / area). She also found that colony status determined swarm width with nomadic colonies having wider swarms. However, none of this work has examined ant size or behavior in swarms.

*E. burchellii* ecology has been well described (Rettenmeyer 1963; Schneirla 1971 and others; Franks 1980; Franks 1982a; Franks and Bossert 1983; Franks and Fletcher 1983; Gotwald 1995; Denny et al. 2004). A number of researchers have also added details to Schneirla’s work but these subsequent efforts have primarily examined other parts of the foraging process such as prey retrieval (Franks 1985; Franks 1986; Franks et al. 1999; Powell and Franks 2005), capture success (Otis et al. 1986; Powell and Franks 2005; Wrege et al. 2005), swarm intensity (Swartz 1997) and trail running behavior (Couzin and Franks 2003; Powell and Franks 2005). More recently, Couzin and Franks (2003) used manual measurements from video recordings of *E. burchellii* trail systems to model trail formation. Their results indicate that ant interactions at high ant densities play an important role in trail formation, but their work did not address ant behavior within swarms.

Fitness of *E. burchellii* colonies is believed to be largely dependent on resource availability (Schneirla 1971; Franks 1985). *E. burchellii* foraging has high energy requirements and the ants must accomplish their foraging under a number of substantial time constraints. First, *E. burchellii* is a diurnal forager giving it only about 12 hours to complete its entire foraging effort. Secondly, because colonies are nomadic for two out of every five weeks, following every day’s foraging effort, the ants must relocate the entire colony including the brood and queen to a new nest 50-100 meters away (Burton and Franks 1985; Bartholomew et al. 1988; Partridge et al. 1996; Franks et al. 1999; Boswell et al. 2001; Powell and Franks 2005; Wrege et al. 2005). This suggests that there is considerable evolutionary pressure to increase foraging efficiency through optimization of the individual behavioral rules that determine swarm behavior. Additionally, observations on captive colonies indicate that *E. burchellii* uses only ground-based pheromones and physical recruitment for prey capture (T. Brown, unpublished data); there is no other evidence that they have any fast-acting airborne recruitment pheromone for prey capture (Torgerson and Akre 1970b; Witte and Maschwitz 2002). If this is the case, capture of large prey items can only be successful in areas with numerous ants present at the time of initial prey contact. As a result, overall capture success and therefore colony fitness in *E. burchellii* is likely highly dependent on how well the ants manage the tradeoff between maximizing the area searched for prey and maintaining sufficiently high local densities to catch prey once detected. Consequently, we hypothesize that the algorithms *E. burchellii* use to organize their swarms will be highly efficient at distributing ants effectively within the swarm.
Better understanding self-organized swarming behaviors also has applications for many non biological fields. Researchers in a wide range of traditionally computer-science or engineering oriented fields such as robotics, data mining and network routing are beginning to appreciate the usefulness of understanding how natural systems solve computational complex problems in decentralized ways (Dorigo and Gambardella 1997; Bonabeau et al. 1998a; Bonabeau et al. 1999; Parpinelli et al. 2002; Dorigo and Stützle 2004). However, current work is largely limited to “biologically inspired” applications (e.g., Dorigo and Gambardella 1997; Bonabeau et al. 1999; Gambardella et al. 1999; Bonabeau et al. 2000; Dorigo and Stützle 2004; Ramos and Abraham 2004). Although these approaches have shown some utility, truly innovative application of social insect algorithms and “swarm” based approaches to computing require a much deeper mechanistic understanding of how self-organization works in biological systems. Our current work seeks to help develop the necessary tools and model systems to provide this understanding.

The spatial and temporal scale of *E. burchellii* swarms make quantitative descriptions of individual-level behaviors quite challenging. *E. burchellii* are very difficult to keep in captivity and it is, as yet, impossible to observe large-scale swarming behaviors in the lab. Although automatically tracking ants in a controlled lab environment is possible (Fourcassié and Traniello 1995; Gordon 1995; Couzin 1999; Balch et al. 2001), no one has developed software robust enough to permit automated tracking of army ants from field video recordings. Consequently, in the 65 years since Schneirla’s seminal work, no one has attempted to quantify Schneirla’s description of the internal dynamics of *E. burchellii* swarms.

The central focus of our work was to identify and quantitatively describe larger scale swarm-level patterns and the overall spatial distribution of ants within *E. burchellii* swarms, and to determine a minimal set of behavioral rules for swarming in *E. burchellii*. In addition, we sought to use data obtained in this current work to parameterize an individual based model of *E. burchellii*. Such a model will allow us to rigorously test if the swarming rules described in this work can reproduce measured patterns and ant distributions. Results from our modeling work will be presented in a forthcoming publication.

Our specific research questions were the following:

1) How do pheromone and density affect turn angle and speed in individuals and what are the relative strengths of these effects?

2) Do ants of different sizes or at different locations in the swarm follow different behavioral rules?

3) Is there is any stratification by size or other physical factors within the swarm?

4) What role, if any, do self-organized processes play in *E. burchellii* swarm organization?
Materials and methods

Field data collection

Field data collection took place during the rainy season (July, 2002) in the rainforest surrounding Sirena Research Station, Corcovado National Park, Costa Rica. *Eciton burchellii* army ant swarms were filmed with a Sony single-chip digital video camera. Swarms were videotaped by placing the video camera on a tripod in the path of an approaching swarm front prior to the arrival of the first ants. The camera was placed approximately 45 centimeters above the ground with the lens facing straight down, parallel to the ground. The area recorded by the camera was 41.6 centimeters wide and 27.6 centimeters high. Video was recorded from the arrival of the first ants in the swarm until the densest part of the swarm had passed. Video clips ranged from about 2 to 4.5 minutes long (~3,600 to 7,500 frames at 29.97 frames per second).

Data collection from video

Choice of video clips

Video clips of two swarms were analyzed. Clips were chosen that appeared to approximate a “typical” raid pattern while minimizing noise from to extraneous factors. In the chosen clips, ant density changed from no ants present to high ant densities, the ants moved predominantly from the top to the bottom of the screen with minimal side entry and the trails formed were clearly delineated and mostly parallel. The forest floor in the clips was largely flat leaf litter with some small sticks. A quantitative summary of the data collected from the two clips is presented in Table 2.

Table 2 Summary of data collected from video clips.

<table>
<thead>
<tr>
<th></th>
<th>Clip 1</th>
<th>Clip 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colony status</td>
<td>Nomadic</td>
<td>Nomadic</td>
</tr>
<tr>
<td>Clip length in seconds</td>
<td>252</td>
<td>204</td>
</tr>
<tr>
<td>Clip length in frames</td>
<td>7651</td>
<td>6051</td>
</tr>
<tr>
<td>&quot;Density&quot; dataset</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area measured</td>
<td>502 cm²</td>
<td>566 cm²</td>
</tr>
<tr>
<td>Total ants marked</td>
<td>12,132</td>
<td>7,453</td>
</tr>
<tr>
<td>Min ants per frame</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Max ants per frame</td>
<td>325</td>
<td>197</td>
</tr>
<tr>
<td>Max ants per cm²</td>
<td>0.65</td>
<td>0.34</td>
</tr>
<tr>
<td>Number of frames where density was measured</td>
<td>154</td>
<td>121</td>
</tr>
<tr>
<td>&quot;Paths&quot; dataset</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total paths tracked</td>
<td>154</td>
<td>47</td>
</tr>
<tr>
<td>Path length (frames)</td>
<td>155 (726, 26)</td>
<td>138 (352, 15)</td>
</tr>
<tr>
<td>Mean (max, min)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Ant tracking software

To measure ant behavior, we created tracking software with Microsoft’s Visual Basic 6.0. The tracking software permits manual collection of total numbers and body angles of ants in individual frames of video (“density” data) and position data for individual ants over multiple frames (“path” data). Collectively, these data provide a profile of ant density, body and turn angles, speeds, and paths within a temporal cross-section of a swarm. Repeated measurements by multiple observers suggest that ant position data were accurate to within 2 millimeters.

Density data

To collect density data, we drew an arbitrarily positioned rectangular box over the center of each video clip. For every 50th frame (e.g., frame 1, 51, 101, etc.) the pixel coordinates for the head and tail of every ant present within the box was recorded. Ants were only marked if both head and tail were within the lines of the box. Ants that were hidden under leaves or in shadows were only marked if their position could be easily made out or if they emerged or disappeared within a few frames of the frame being measured. Collectively, the density data enable measurement of ant density throughout the swarm front, the mean length of ants in different parts in the swarm and the mean and standard deviation of ant body angles relative to the screen. We also used the head-tail coordinate data to calculate ant body angles relative to the screen (“absolute” angle) and relative to mean direction of all ants in a frame. Standard deviation of all ant body angles in a frame provided a global measure of “cohesion” of direction for the swarm. Standard deviation of body angle goes down as the number of ants going in the same direction increases.

Path tracking

Individual ant trajectories were tracked over time by recording the ant’s coordinate head and tail position any time the ant moved, stopped or changed its body angle significantly (usually every few frames). To control for potential selection bias, the top area of the screen was broken into four quadrants and an effort was made to continuously track an ant originating from each of the quadrants. Individuals were tracked from when they appeared on the top of the screen until they were lost from view. When an ant was lost from view, the next ant to appear at the top of that quadrant was chosen. Ants were not tracked if they were visible for less than 15 frames and an effort was made to choose paths that were somewhat longer than this (Table 2).

In the early frames of each clip when ant density was low it was possible to track the path of every ant as it appeared on the screen. As the number of ants present became prohibitively large, an average of three to five ants in clip 1 and one to two ants in clip 2 were tracked at any given moment. In later frames, ants were generally tracked for shorter distances before being lost, due to the high density of ants.

As recorded, the ant path data required the following processing steps to be usable (Fig. 2). First, the mean length of the ant was calculated from all length measurements in the path. Second, the mid-point position and body angle of the ant was calculated at each
frame where it was measured. Third, the ant’s mid-point position and body angle at intermediate frames between measured points was calculated using linear interpolation. Finally, new head and tail positions were calculated for the ant using the mean ant length and the current body angle measured for a path, at every frame in that path.

<table>
<thead>
<tr>
<th>Raw Path: Ant Position recorded every 2-3 frames; ant</th>
<th>Step 1: Calculate mean path length.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Step 2: Find mid-points for measured ant positions.</td>
</tr>
<tr>
<td></td>
<td>Step 3: Interpolate between measured positions to get mid-points and body angles for intermediate frames</td>
</tr>
<tr>
<td></td>
<td>Step 4: Create final path. Calculate new head and tail position for all frames based on mean length and interpolated body angle</td>
</tr>
</tbody>
</table>

Fig. 2  Conversion of raw path data into smoothed paths with data at every frame.

Following processing, path data was analyzed as follows: At each frame (0.033 second) in each ant path tracked, we recorded ant length, speed, the pheromone values under each antenna at the previous and current frame and ant angle. Two types of angles were recorded from path data. Turn angle (“relative” angle) is a measure of how much an ant turned from its previous position. Body angle (“absolute” angle), just as in the density data, is a measure of the ant’s body angle relative to the screen. An ant with a body angle of zero is facing straight down. At each time step, we also calculated the “angle difference,” which was the difference between individual body angles of ants in the paths dataset and the mean angle of all density ants at the nearest frame where density was measured. This provided a gauge of how closely turn angles of individual ants conformed to overall swarm direction. The standard deviation of absolute ant body angle relative to the screen (“absolute” angle) is a measure of how consistently the ant behaves. Paths of ants that turn frequently have a high standard deviation of body angle; paths of ants that ran straighter have low standard deviation of body angle.
Pheromone mapping and parameter estimation

Pheromone diffusion on substrate

There is currently no direct way to measure the chemical landscape experienced by army ants in the field. In addition, no data exist on the quantity or rate of pheromone deposition in *E. burchellii*. As a metric for pheromone concentration, cumulative number of ants passing a given point was used. All ant positions from both density and path data were used together to estimate “pheromone” values because neither measure on its own provided sufficient data. The density data provide the most even coverage of ant positions but is less accurate than path data because ants move ~4 centimeters per second and density data were sampled only every 50 frames (1.7 seconds). This is problematic because in the time between our samples an ant can leave a 7 centimeter long trail but the sampling will only have recorded two points. This is particularly a problem in earlier frames when the influence of paths left by single ants is high. Path data are thus more accurate in early frames because the path data records the complete path left by every ant. In later frames, when ant density is high, the path data are less accurate because only one to two percent of total ants present are being tracked. In these later frames, the density data provide a better representation of the pheromone landscape because they accurately sample ants at every position on the substrate. By combining the datasets, we sought to average the errors inherent in each sampling method.

Using the software package Matlab (Version R14) we created a 2 millimeter-scale grid the size of the area sampled. We assumed that all ants leave a single unit of pheromone at each time step. Beginning with the first frame of the video, one unit of pheromone was added at each coordinate position where there were ants at that time in the density or path data. Because density data were sampled only every 50th frame, while path data were sampled every frame, path data from intermediate frames were collated and added concurrently at the frame corresponding to the nearest density frame.

In order to mimic the spread of the pheromone signal over the substrate and to smooth out the effects of our two sampling methods, we applied the pheromone diffusion equation (equation (1)) developed by Calenbuhr et al. (Calenbuhr et al. 1992; 1992; Couzin and Franks 2003). At every time step, equation 1 was applied to the pheromone grid. $C(r, \tau)$ is the concentration of pheromone at distance $r$, and time $\tau$. Units of the diffusion coefficient $D$ are $\text{cm} / \tau$. Time step was five frames (0.17 seconds); this was the shortest computationally feasible time step.

$$C(r, \tau) = \frac{1}{4\pi D \tau} \exp \left( -\frac{r^2}{4D\tau} \right)$$

Equation (1)

Numerical analysis of equation 1 shows that it is highly sensitive to the chosen diffusion coefficient $D$. However, little is known about the diffusion of *E. burchellii* pheromone on substrates or in the air (Akre 1965; Torgerson 1969; Torgerson and Akre 1970a; Torgerson and Akre 1970b; Billen 1985; Morgan et al. 1994; Oldham et al. 1994; Billen and Gobin 1996 and see Chapter 3). To pick the best diffusion coefficient, we analyzed the model fit for ant turning response to pheromone concentrations in clip 1.
using diffusion values across three orders of magnitude, centered around the values used in previous studies (0.1 to 0.0001) (Calenbuhr and Deneubourg 1992; Couzin and Franks 2003). The diffusion coefficient that yielded the best AIC values (Burnham and Anderson 2003) for the model fit was used for subsequent analyses in both clips.

Antennae length

Because *E. burchellii* are almost blind, they primarily perceive external stimuli such as pheromone and density with their antennae (Schneirla 1971). Consequently, to determine the pheromone landscape experienced by the ants, it is necessary to know how far ahead an army ant can perceive with its antennae. However, only limited data exist on perceptive distance in *E. burchellii* (Topoff and Mirenda 1975; Couzin and Franks 2003) and no data exist on length of antennae. Based on previous literature, we chose a fixed antennae length of 4 millimeters (Couzin and Franks 2003).

Turning behavior with pheromone

To connect the path data with the approximated pheromone map, ant antenna positions were calculated for each frame in a path. For simplicity, antennae were assumed to protrude from the ant’s head at a 45 degree angle (Couzin and Franks 2003). For each ant path, at each timestep, the pheromone concentration under each antenna was sampled from the nearest frame of smoothed pheromone. Ant speed, the amount it turned from the previous step (“relative” angle) and body angle relative to the screen (“absolute” angle) were also calculated. Relative body angle is measured as the change in body angle from the ant’s previous position. Relative body angle provides a measure of how much an ant turns per step. Standard deviation of absolute angle per path gives a measure of the straightness of an ant’s path overall. “Total pheromone” per step was calculated as the sum of the approximate pheromone amount measured under each antenna.

Effects of mean frame density and mean body angle on tracked ants

To measure how overall density affected ant turning behavior, number of ants in a frame from the “density” data was included as a factor in our analyses of ant paths and turning behaviors. We also examined how the body angles of ants at each step in a path differed from the mean body angle of all ants in the nearest frame where density was measured. This provides a measure of the swarm’s “cohesion” and overall direction of travel.

Data and statistical analyses

All output from the tracking program was analyzed using Matlab. All statistical analyses were performed using the open source statistical package R (Version 2.1.0, http://www.R-project.org). For analyses that included path data that was sampled by frame, the effects of path were randomized using a linear mixed effects model with ant path number as the random effect. All other analyses were fitted with a standard linear model. Mean body and turning angles were calculated using the circular statistics package “CircStats,” in R.
Results

Estimation of diffusion coefficient

Results for all diffusion values tested were highly significant. The diffusion coefficient $D$ that yielded the best model fit ($D = 0.002$; $p = 0$, AIC = -29228.66) was used for all subsequent analyses in both clips. Because our data were collected on timescales of less than 5 minutes (Table 2), the effects of evaporation were not considered to be significant (Torgerson and Akre 1970b).

Video data

Trajectories of tracked ants are presented in Fig. 3. Time (i.e., video frame number) provides a metric for position in the swarm because the swarm was filmed as it passed under the camera. By comparing observed densities with what is known about swarm structure it is possibly to roughly match our data (Fig. 1, Fig. 4) with the generalized map of the swarm (Fig. 1). Thus early frame numbers describe the front of the swarm (Fig. 1 and Fig. 4, regions A and B) and later frames represent events taking place in the middle or back of the main swarm (regions C and D). Our video recordings did not capture the fan area (Fig. 1 E).

Fig. 3  Cumulative trajectories of all tracked ant paths for clip 1 (axes in centimeters). a All paths from $t = 0$ to $t = 117.4$ seconds (frame 3500). b All paths from $t = 0$ to $t = t = 183.5$ seconds (frame 5500). c All paths, entire clip; $t = 0$ to $t = 255.3$ seconds (frame 7651). Tracked ants were chosen randomly. Note that in this clip, major paths appear to be laid very early on by pioneer ants and maintained throughout the passing of the swarm front.

Pheromone map

A 2 millimeter-scale map of estimated pheromone concentration over time was generated using position data for all ants in both density and path datasets. This provides a three-dimensional map of the approximate pheromone landscape experienced by the ants over time.
Absolute angle and ant density

Maximum ant densities were approximately twice as high in clip 1 as in clip 2 (Table 2 and Fig. 4). In both clips, standard deviation of ant body angles per frame in the “density” dataset decreases significantly with both frame and overall density (Fig. 4 a and b). In both clips, standard deviation of body angle drops abruptly when ant density exceeds 2.5 ants / 10 cm² and then rises again when density drops below this threshold at the back of the swarm. We believe this indicates the point at which density effects begin to outweigh turning response to pheromone. To examine the effect of density on cohesion in the swarm, within the data where ant density was over 1 ant / 10 cm², we examined the relation between number of ants in a frame and the standard deviation of the body angles of all ants in that frame. Number of ants in the area significantly determines the “cohesion” (measured by standard deviation of all ant body angles) within the swarm (Fig. 4b and c).

Ant length

In both clips, mean ant length decreased significantly with time (Fig. 5). Although the number of long ants present decreases slightly over time, the decrease in mean length is primarily driven by an increase in the number of small ants (Fig. 5). The length of the shortest ants present also decreases over time.
Effect of position in swarm on net-to-gross displacement ratio (NGDR), clip 1

Net-to-gross displacement ratio (NGDR) provides a measure of the circuitry of an organism’s path. NGDR was calculated by discretizing each path into \( \frac{1}{2} \) second (15

Fig. 4  Standard deviation of ant body angles, total ant numbers per frame and circular deviation of ant body angles by density. a, b  Standard deviation of ant body angles and total ant number per frame from the "density" dataset. Ant density and body angles were recorded every 50 frames (clip 1: N = 12,132 ants, clip 2: N = 7,453 ants). Letters denote inferred position in swarm (see Fig. 1). c, d  Ant density (total ants in a frame) significantly determines cohesiveness of body angle (Clip 1, \( p < 2 \times 10^{-16}, N = 6,983 \) ants, 62 frames; Clip 2, \( p < 2 \times 10^{-10}, N = 12,132 \) ants, 154 frames). In clip 1 (c), time does not significantly affect standard deviation of ant body angle. In clip 2 (d), time also affects standard deviation of body angle (\( p = 0.01 \)).
Temporal cross-section of ant lengths in the swarm. Ant length over time (dots) and mean ant length per frame (line) of all ants in both clips decreases significantly with time (clip 1: $p < 2 \times 10^{-16}$, $N = 12,132$ ants; clip 2: $p = 1.4 \times 10^{-6}$, $N = 2,454$). In clip 1, ants were sampled every 50 frames ($N = 154$ frames); in clip 2, ants were sampled approximately every 250 frames ($N = 39$ frames).

Frame (segments) and dividing the distance between the ant’s starting and stopping point in each segment by the total linear distance the ant traveled in that time period. A low NGDR indicates that an ant is turning frequently because the distance it moves between start and stopping point is much shorter than the linear distance the ant traveled. An NGDR of 1 indicates that an ant is not turning at all. We analyzed NGDR for clip 1. In clip 1, NGDR increases significantly with time indicating that ants turn less later in the swarm ($p = 1.2 \times 10^{-7}$, $N = 1,569$ 15-second segments from 154 paths). Length had no significant effect on NGDR ($p = 0.7$).

**Length and speed**

The path data indicate that longer ants ran significantly faster at all times in both clips (Fig. 6, Table 3). In addition, the mean speed of all pioneer ants, independent of size, is significantly faster than that of ants in the front of the swarm (Fig. 7, Table 3a). In both clips, log ant speed increases at approximately the square root of log ant length (Clip 1, 0.45; Clip 2, 0.64).

**Pheromone effects on speed**

Increased density and amount of “pheromone” each reduce ant speed (Table 3a). However, when both pheromone and density are high, ant speed increases. To explore this interaction we split the data into ants measured before and after density exceeds 2.5 ants / 10 cm$^2$. This is when strong density effects appeared in the density dataset as indicated by the dip in standard deviation of body angle (Fig. 4, clip 1: $T \approx 183$, clip 2: $T \approx 130$). Ants before this cutoff were labeled “early” ants; ants after were “late” ants.
Early ants (Fig. 8, Table 3 c): Early ants ran significantly faster when there was less pheromone (Fig. 8, solid lines, solid circles). In clip 1, total pheromone also has a greater positive effect on ant speed for larger ants. Overall, ants in frames with higher density ran more slowly, but ants in areas with high pheromone and high density ran faster.

Fig. 6 Mean ant length and running speed. Mean speed of longer ants is faster even after controlling for position in swarm (Table 3; clip 1: N = 154 paths, p < 0.03; clip 2: N = 47 paths, p < 0.001).

Fig. 7 The mean speed (closed circles) and standard deviation (SD) of speed (open circles) per path is higher for pioneer ants in both clips (Table 3 a,b). Mean path speed is plotted at the mean frame number of each path in seconds.

Late ants (Fig. 8, Table 3 c): For late ants, the effect is reversed and mean ant speed increased with increasing pheromone (Fig. 8, dashed lines, open circles). For late ants in clip 1, total pheromone, ant density, ant length, and the interaction between total
pheromone and density all positively affected speed. No results were significant for late ants in clip 2.

Pheromone, turn angle and density effects

Ants turn towards higher pheromone (Fig. 9 solid lines, Table 4) and this effect is highly significant (p < 2 * 10\(^{-16}\)). The strength of the turning response is reduced as both total pheromone present and ant density increase. The difference of the ant’s body angle from the mean body angle of all ants in the frame also affects turning both by itself and as a positive interaction with the amount of pheromone present (Table 4). Thus when pheromone and densities are high (i.e., in the main part of the swarm, Fig. 1 C), ants tend to react more to their neighbors than to the pheromone signal they experience. Longer ants are less affected by this interaction (Table 4).

Table 3  Factors determining ant speed.\(^1\)

a Mean ant speed

| Clip 1 | Estimate | Std. Error | t-value | Pr(>|t|) |
|-------|----------|------------|---------|---------|
| (Intercept) | 3.32244 | 0.63058 | 5.269 | 4.73e-07 |
| Length | 2.44787 | 1.07910 | 2.268 | 0.024740 |
| Total pheromone | -0.25157 | 0.07196 | -3.496 | 0.000623 |
| Frame Density\(^2\) | -0.32047 | 0.11845 | -2.706 | 0.007614 |
| Total pheromone : Frame density | 0.08299 | 0.02623 | 3.164 | 0.001886 |

| Clip 2 | Estimate | Std. Error | t-value | Pr(>|t|) |
|-------|----------|------------|---------|---------|
| (Intercept) | -4.891 | 2.522 | -1.940 | 0.058868 |
| Length | 16.598 | 4.437 | 3.741 | 0.000527 |
| Total pheromone | 4.410 | 1.397 | 3.157 | 0.002879 |
| Length : Total pheromone | -8.683 | 2.655 | -3.270 | 0.002091 |

b Standard deviation of ant speed per path. Standard deviation of speed is a measure of how much an ant stops and starts.

| Clip 1 | Estimate | Std. Error | t-value | Pr(>|t|) |
|-------|----------|------------|---------|---------|
| (Intercept) | 0.38309 | 0.10711 | 3.577 | 0.000469 |
| Length | 0.19343 | 0.19705 | 0.982 | 0.327850 |
| Frame density | 0.11130 | 0.05962 | 1.867 | 0.063876 |
| Length : Frame density | -0.25921 | 0.11794 | -2.198 | 0.029498 |

| Clip 2 | Estimate | Std. Error | t-value | Pr(>|t|) |
|-------|----------|------------|---------|---------|
| Results not significant | -- | -- | -- | -- |
Table 3 Continued

c Factors determining mean ant speed for early and late ants.

| Early ants | Estimate | Std-Error | t-value | Pr(>|t|) |
|------------|----------|-----------|---------|----------|
| Clip 1     |          |           |         |          |
| (Intercept)| 6.7484   | 1.4801    | 4.559   | 1.37e-05 |
| Length     | -3.6398  | 2.6251    | -1.387  | 0.16847  |
| Total pheromone | -1.7249 | 0.5601    | -3.080  | 0.00263  |
| Length : Total pheromone | 2.5946 | 0.9943    | 2.610   | 0.01036  |

| Clip 2     |          |           |         |          |
| (Intercept)| 3.508    | 3.571     | 0.982   | 0.339    |
| Length     | 12.922   | 4.713     | 2.742   | 0.013    |
| Frame Density | -33.773 | 9.441     | -3.577  | 0.002    |
| Total pheromone | -8.904 | 2.336     | -3.811  | 0.001    |
| Total pheromone : Frame density | 45.424 | 12.590    | 3.608   | 0.002    |

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| Clip 2     |          |           |         |          |
| Results not significant | -- | -- | -- | -- |

Notes:
1 Initial linear model included all two-way interactions between ant’s speed and the following factors: Ant length, total pheromone experienced per path and frame density.
2 Frame density = Density of ants in nearest “density” frame.
Fig. 8  In the early part of the swarm (solid lines, closed circles), mean path speed is faster with lower pheromone. In high-density areas (dashed lines, open circles), mean path speed is faster with higher pheromone (Table 3 b).

Fig. 9  Ants turn towards higher pheromone (Table 4).
Table 4  Factors determining ant turn angle.1

<table>
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<tr>
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Notes:
1 Initial linear mixed effects model included all two-way interactions between ant’s turn angle and the following factors: total pheromone, frame density, “prevpherdiff,” ant length and angle difference. Effect of individual ant paths was randomized.
2 Prevpherdiff. = Difference in pheromone concentration between antennae at previous step
3 Angle difference = Difference in ant’s body angle from mean body angle of all ants in nearest “density” frame.
4 Total pheromone = Sum of pheromone values under each antennae at previous step.
5 Frame density = Density of ants in nearest “density” frame.

Discussion

The examination of army ant swarming rules addresses fundamental biological questions about the organization and evolution of complex living systems. *E. burchellii* colonies face a number of significant optimal foraging problems. First, the ants must distribute themselves evenly enough to find fast running, diffusely distributed prey items. Second, they must maintain local densities sufficient to capture prey items once discovered. Third, they must create and maintain a cohesive trail system to retrieve prey items to the nest and keep the swarm sufficiently supplied with ants. *E. burchellii* have a very simple set of tools to solve the above problems and they are energy limited, almost blind and have little or no sense of direction. Yet despite all this, *E. burchellii* is a top arthropod predator in tropical forest ecosystems (Franks and Bossert 1983). *E. burchellii* can sense and move up pheromone gradients (Fig. 9), react to density and the direction of their neighbors (Fig. 4) and run at different rates based on size (Fig. 6), and pheromone levels (Fig. 8). Our results provide evidence that variations in these simple behavioral parameters can generate higher-order behavioral patterns such as *E. burchellii* swarming through self-organization.
Pheromone mapping

By creating an approximate mapping of the pheromone landscape experienced by swarming *E. burchellii* ants we have generated the first quantitative description of how army ants respond behaviorally to relative differences in trail pheromone. This method of mapping pheromone required two primary assumptions. First, that all ants, independent of size and position in swarm, lay the same amount of pheromone. There is no work on how much pheromone is laid by army ants based on size or position in swarm. Visual analysis of video of swarming ants suggests that ants in all phases of the swarm (pioneers, ants in main swarm and ants on trails) all perform obvious gastor-touching motions on the substrate as they run, as if laying pheromone. However no work has been done to quantify these behaviors. Our second assumption was that pheromone diffuses laterally on the substrate at the rate modeled in equation (1). We tested the model fit over nearly 50 different values for the diffusion coefficient and all values were highly significant and yielded similar results. Consequently, we believe the values used are a reasonable starting point in the absence of further information. Overall, given the high statistical significance of our results, we feel that our assumptions were biologically reasonable and provide a good starting point for further research.

Pheromone related behavior

Early on, relative amount of pheromone present appears to determine both turning behavior, and, independent of length, determine speed and standard deviation of speed. Later on, ants run more slowly because of increased ant density and higher pheromone levels. As densities rise, ants also run at more consistent speeds (Table 3 a). They are a number of possible explanations for this. First, the ants may run more consistently because ants in denser parts of the swarm have stronger trails to follow. Second, they may run more consistently because high neighbor density prevents them from turning. Finally, increased ant density is well documented to facilitate trail running in *E. burchellii* (Schneirla 1944; Schneirla 1971).

At higher densities, density effects strongly influence ant behavior. We interpret the dip in standard deviation of body angle in both clips (Fig. 4 a and b) as an indication of where density effects start to swamp out the effects of pheromone. For both clips, these effects become noticeable when ant density reaches about 1 ant / 5 cm². This suggests that ants start to avoid each their neighbors when they are within ~2.5 centimeters of each other. This is a similar interaction distance to that found by Couzin and Franks (2003).

Army ant foraging strategies and swarm organization

Larger ants are faster (Fig. 5c) and so presumably can search more ground than can smaller ants in the same time period. They can carry larger prey items (Powell and Franks 2005) and are likely more robust to attack. In addition, our observations on captive colonies suggest that ant size plays a role in capture success (T. Brown, unpublished data). One way for an *E. burchellii* colony to maximize foraging success would be to produce more large ants. However larger ants require more resources to
produce and this cost scales nonlinearly (Franks et al. 1999). Thus from an evolutionary standpoint, one would predict that larger ants would only be used in areas where their increased size provided an essential service (Franks et al. 1999; Powell and Franks 2005). Consequently, our observation that pioneers are predominantly larger ants suggests that their presence in this position is energetically important for the colony.

In the front of the swarm, where there is little or no pheromone (Fig. 1 A), all ants turn frequently. This behavior has at least four important functions. First, by turning frequently, the ants are searching new ground, increasing the likelihood that prey will be discovered and captured or flushed into the main part of the swarm. Second, as the pioneers re-find their own trails and return on them to the swarm, they are building and reinforcing the first outlines of a trail system. In all clips examined, many of the trails that become primary trails after the swarm passed were initially laid by pioneers in the first few minutes of each clip (Fig. 3).

As pioneers return to the swarm, they bump into outgoing ants, slowing them down. This behavior creates what we term an “eddy line.” In flowing water, an eddy line is a transitional area of interaction between a fast and a slow current which creates a distinct barrier between the two flows. Schneirla (1940) suggested that *E. burchellii* army ants have little sense of direction in the swarm front and rely primarily on consensus polling of neighbors to determine which direction to run. Our work also suggests that this is the case. In the ant swarm, the “eddy line” is visually apparent as a semi chaotic region at the front edge of main swarm where there is a high interaction rate between incoming pioneers and outgoing ants. As the two or more ants with different trajectories move around each other attempting to establish a consensus direction, their forward progress is slowed. These interactions form a partial barrier to forward progress by slowing the advance of outgoing individuals in the main swarm. By slowing the progress of the front of the swarm, this behavioral barrier flattens the swarm front and helps to maintain high ant densities in the main part of the swarm (Fig. 1 B). The eddy line area is visible in Fig. 8 as the change in slope of the speed response to pheromone for early and late ants. Early ants run more slowly as pheromone increases, presumably due to interactions with other ants. Ants in areas behind the eddy line and farther back in the swarm are able to run faster as all ants are increasingly on trails and running in the same direction. The mean speed of ants in the swarm front and at the back of the swarm is similar to those measured by other researchers for unburdened ants running on well laid-in trails (4-5 cm / sec, Willis 1967; Topoff et al. 1972a; Topoff et al. 1972b; Franks et al. 1991; Billen and Gobin 1996; Swartz 1997; Powell and Franks 2005). This suggests that at the back of the swarm, similar processes to those found by Couzin and Franks may be taking place (Couzin and Franks 2003). Their model results indicated that the neighbor-avoidance behavior of ants running in high-density areas causes spontaneous formation of lanes which results in optimized traffic flow.

It is unclear if the high turn frequency exhibited by pioneer ants in low pheromone areas is a distinct “searching” behavior or if the ants are just turning in response to lack of trail pheromone. In our observations of videotaped swarms, pioneers act as if they are actively searching – stopping and starting frequently, moving briefly under leaves and then reversing direction, etc. In the data, these behaviors are apparent,
globally, as a high standard deviation of ant body angles per frame (Fig. 4), and individually, as a high standard deviation of speed in early paths (Fig. 7). However, it remains to be seen if the ants really “search” intentionally or if search-like behaviors are merely a result of the ant’s increased turning behavior in the face of low pheromone.

After the pioneer ants have passed through an area and laid down the initial rudimentary structure of a trail system, the smaller, more numerous ants arrive, filling in the gaps and covering the ground (Fig. 5). In the densest part of the swarm (Fig. 1, C) an interesting interaction between pheromone and density effects takes place. In this part of the swarm, a number of areas have noticeable trails (Fig. 3). However, at higher pheromone levels, ant turning response to pheromone is reduced both due to the presence of higher pheromone amounts and high ant densities (Table 3) which prevent ants from turning towards the higher pheromone as much as they normally would. As a balance develops between these competing forces, the ants effectively distribute themselves in space.

At the back of the swarm, ant density has begun to decrease overall, but incoming trails are still over-full with ants (Fig. 1, Fig. 4, D). In addition, the passing swarm has left a low level of pheromone covering much of the substrate. As ants arriving on the trunk trails approach this area, density becomes high enough that they are likely to be pushed off of trails. As they leave the trails, they find themselves in areas with reduced ant density and some pheromone everywhere but no clear trail signal. The weak, but widely distributed pheromone causes the ants’ turning rate to increase somewhat. As a result, ants in the back of the swarm continue to move forward while searching the area until they again find a trail. We believe that this behavior helps to create a “mop-up” operation where arriving ants at the back of the swarm search the area where the swarm has passed to help find any remaining prey items.

Size-related behaviors

Although submajors make up only 3% of the colony, Franks (Franks et al. 1999) found that they constitute 25% of the ants involved in prey retrieval. Recent work (Powell and Franks 2005) has made a strong case that the submajor class has specifically evolved in *E. burchellii* in order to improve foraging efficiency, in particular prey retrieval. The results of our work suggest that longer ants may help improve swarming efficiency as well. There are a number of reasons why it may make sense for the colony to allocate less numerous, higher cost workers to the front of the swarm. First, longer ants have disproportionately longer legs and run faster and more efficiently (Bartholomew et al. 1988; Feener et al. 1988; Franks et al. 1999). At the front of the swarm, as noted earlier, they are able to cover ground more quickly than shorter ants which means they can search a larger area in a shorter period of time. This in turn means the swarm can move forward more quickly. Larger ants may also be better able to prevent the escape of larger prey in low density areas where it can take some time for other ants to arrive and help immobilize a prey item. It should be noted that submajors are rarely found make up less than 1% of the swarm front. Analysis of our length data (Fig. 5) suggests that the majority of the long ants in the swarm are ants at top end of the length spectrum for the worker class (Scott Powell, unpublished data).
Although longer ants clearly run faster (Fig. 6, Table 3a), it is less clear if they behave differently in other ways as well. Net-to-gross displacement analysis shows no effect of length (p = 0.7). But other results hint that longer ants may behave differently. Length does appear, usually as an interaction effect, in a number of our analyses (Table 3), but results are not consistent between clips. In addition, anecdotal observations on captive colonies suggest that larger ants are less sensitive to avoiding low pheromone areas. However, mean pheromone experienced per path was only significantly determined by length in clip 2. These questions need to be addressed in future research.

Characteristic swarm patterns and spatial distribution

As noted earlier, Schneirla (Schneirla 1940) argued that *E. burchelli* lacks any sense of direction and that the forward movement of the swarm is generated entirely through excited ants running in the same direction as their neighbors. This is a striking hypothesis given that raids frequently travel as far as 200 meters with little directional deviation (Swartz 1997). However, Schneirla’s suggestion seems plausible given our results.

A significant problem the ants face in filling space evenly is maintaining even distributions and densities in the main part of the swarm. The traditional assumption has been that the flat-topped shape of *E. burchelli* swarms is predominantly determined by the slowing of pioneer ants in low pheromone areas (Schneirla 1940; Franks et al. 1991). Earlier computer models of *E. burchelli* swarming seem to be largely driven by this mechanism (Franks et al. 1991). Our initial reproduction of these models (Brown 2003) found that without a mechanism to slow down ants at the front of the swarm (e.g., by limiting their speed in low pheromone areas), the ants in the densest part of the swarm stream forward and high densities are not maintained in the main swarm. Our discovery that ants at the front of the swarm are faster and larger overturns the hypothesis that swarm shape is mostly determined by slow pioneers.

It seems likely that rather than being determined by pheromone effects on speed, the characteristic flat-fronted shape of the swarm is created predominantly by the physical interactions between returning pioneer ants and outward moving ants. This effect was noted by Schneirla (1940) in his description of swarming behavior. However, Schneirla did not explore the difference between the impact of ants slowing due to low pheromone and the effects of their increased turning behavior and physical interactions with outgoing workers. Subsequent work has primarily assumed that *E. burchelli* runs more slowly in lower pheromone areas and to our knowledge, no one has further examined the relationship between outward pressure and incoming ants.

The effect of an “eddy line” or interaction area at the front of the swarm also provides an explanation for how swarms make the often sudden decision to retreat. This phenomenon is quite striking when observed in the field. In a matter of minutes, a dense outward moving swarm of tens of thousands of ants completely switches direction and all ants begin heading back towards the bivouac. It is possible to follow this state change as the zone of returning ants bumps into the outward running ants on the trunk trail and the outgoing ants in turn change direction. Our explanation for this phenomenon, following
from our results and Schneirla’s work, is that when the outward pressure of ants has become sufficiently reduced from lack of recruitment, the directional force of returning ants overwhelms the outgoing ants resulting in a switch in the consensus direction of movement towards returning to the bivouac.

If it is true that *E. burchellii* has no significant internal sense of direction, this would be a remarkable discovery given the linearity with which their foraging columns proceed. Monica Swartz (1997) quantified this linearity by measuring the difference in angle between starting direction and the direction the swarm was heading at its farthest extent and found a mean variation of only 22° (N = 32, standard deviation = 4.7). She suggested that consistency of foraging direction serves an evolutionary purpose by minimizing the overlap between successive foraging days, particularly when the colonies are in their non nomadic, statary phase.

**Unmeasured factors influencing swarm behavior**

A number of factors that were unmeasured in our data are known to play an important role in swarm processes in *E. burchellii*. Substrate has been shown to play an important role in determining where trails develop (Schneirla 1940) and in determine running speed (Powell and Franks 2005). Although the substrate in the clips analyzed was not highly varied, leaves and sticks did appear to play a role in determining path location. These effects were not accounted for in our analysis.

Colony status (i.e., statary or nomadic) and ant excitement also influence swarm behavior. When colonies are in their nomadic phase, they swarm more intensely and for longer periods of time. This change in swarm intensity is believed to be precipitated by increased ant excitement caused by the feeding demands of thousand of newly hatched larvae (Schneirla 1971). It is unknown what effect this change in activity has on responsiveness to pheromone or the other factors measured in our current work. Our observations on captive colonies suggest that “excitement” levels in individuals play a significant role in swarming behavior and in scaling ant responsiveness to pheromone and prey (T. Brown, unpublished data).

A number of workers have reported significant behavioral differences between colonies (Powell and Franks 2005, M. Swartz, pers. comm.). Both of the swarms videotaped for our research came from the same nomadic colony. Further work is required to determine if there are intercolony differences in the behavioral parameters we measured.

**Self-organization as mechanism for group decision-making**

Swarming in *E. burchellii* is self-organized in that the spatial distribution of ants in the swarm emerges from individual behaviors such as turning response to pheromone and neighbor avoidance. The directional polling described above provides an elegant example of why self-organized processes are fundamentally important in systems such as army ants. There are a host of challenges faced by social insects that require some means to make group decisions, the outcomes of which have significant implication for colony success. However, most social insects can only communicate across small spatial scales.
This leaves organisms such as army ants with no direct means to choose initial direction of foraging, measure factors such as colony satiation, maintain foraging direction, determine length of time to spend foraging etc. In the case of *E. burchellii* foraging, a very simple mechanism – that ants’ directional choices come from that of their neighbors – provides a highly robust solution to all of these problems without the need for any global information exchange or a centralized controller. This process is self-organized because emergent behaviors such as the decision of the swarm to return to the nest are generated by the outcome of thousands of small decisions made between individuals with only local knowledge. No single decision holds significant importance, but when summed over all interactions, the entire swarm of tens of thousands of ants is able to make a consensus decision and switch directions in a few minutes. Self-organized processes such as these have important evolutionary implications because they provide a mechanism by which highly complex group behaviors such as *E. burchellii* foraging can be acted on by natural selection.

**Modeling work**

Few attempts have been made to model army ant swarm behavior and most models incorporate only limited biology (Deneubourg et al. 1989; Franks et al. 1991; Watmough and Edelstein Keshet 1995; Solé et al. 2000). Initial modeling work by Deneubourg et al. (1989) showed that simple rules about how army ants responded to pheromone could generate patterns that were visually similar to real swarm patterns. Their work also suggested that interspecies differences in swarming patterns could be generated solely by changes in prey distribution without changing foraging rules. Both of these results indicate that swarm patterns may rely on simple behavioral rules. Although these results are intriguing, the Deneubourg et Al. model incorporated limited biology and produced only qualitative results. The results of our current work provide the quantitative parameters needed to build a detailed, individual-based model of army ant swarming to test the validity of our analytical results.

**Acknowledgments**

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CHAPTER 3

OPTIMIZED SPACE FILLING IN NEW WORLD ARMY ANT SWARMS

Abstract

Swarming in the New World army ant Eciton burchellii is energetically intensive and time-limited and 50% of the ant’s prey consists of large, highly mobile arthropods with good eyesight. To effectively capture such prey E. burchellii must organize more than 100,000 nearly blind individuals in a rapidly moving 30 m² swarm. Successful swarming requires the ants to balance contradictory objectives. Within the swarm, the ants must maintain an even distribution over as large an area as possible while avoiding over-dispersal or clumping. At the same time, the ants are highly sensitive to trail pheromones and must develop and maintain an extensive trail system linking the swarm to the nest through highly variable terrain. Analysis of data collected from digital video of E. burchellii swarms indicates that E. burchellii distribute themselves evenly in space while maintaining sufficient density within the swarm that larger prey items have close to 100% probability of detection. Finally, based on extensive observations of prey capture in two captive colonies, we describe the primary factors that influence capture success at a local level.

Introduction

Overview

The challenge of optimally allocating foraging effort to maximize fitness is a problem faced by all resource limited organisms (MacArthur and Pianka 1966). Resource availability is often heterogeneous in space and time and individuals must allocate foraging effort based on incomplete predictive maps of their environment. Group foraging and resource pooling can reduce this problem both because individuals can share information to aid in locating resources and because groups can sustain higher levels of individual failure (Chilton and Sealy 1987; Seeley 1995; Ballance and Pitman 1999; Fraser et al. 2006). In addition, group member foraging efforts can be distributed over space or time which improves individuals’ access unpredictable resources (e.g., Chilton and Sealy 1987; Ryer and Olla 1992; Seeley 1995; Ballance and Pitman 1999; Adler and Gordon 2003; Stenberg and Persson 2005). Group foraging also provides the potential for organisms to capture or retrieve prey items that could not be captured by an individual alone (Traniello and Beshers 1991; Traniello and Rosengaus 1997; Powell and Franks 2005).

An interesting variation on group foraging is found in social insects. The genetic structure of social insect colonies – a reproductive queen with sterile workers – allows social insects to employ a number of unique and highly successful foraging strategies. First, although the colony is reproductively a single organism, its foraging body (the workers) is separated from its reproductive body (the queen). This allows a single colony to enjoy the fitness benefits of searching for food in multiple places at the same time.
Second, social insects can employ foraging strategies that maximize colony success despite being individually suboptimal (Adler and Gordon 2003). Finally, because workers do not reproduce and are of relatively low cost to produce (Oster and Wilson 1978), social insects can employ riskier individual foraging strategies than can individual organisms that must directly protect their own reproductive abilities.

However, social insects must overcome a number of challenges if they are to successfully exploit the above strategies. In particular, they must have a way to globally process information about colony food needs, spatial and temporal availability of unpredictable resources, and the spatial distribution of foragers. Nonetheless, the success of social insects is indisputable (Hölldobler and Wilson 1990; Wilson 1990; Seeley 1995) and it has been well documented that many tropical ant species are top consumers in the rainforest. Leafcutters, for instance, have been shown to harvest some 12-17% of forest leaf production (Lugo et al. 1973; Cherrett 1986; Hölldobler and Wilson 1990).

Foraging in the New World army ant *Eciton burchellii*

This chapter examines the foraging strategies employed by the New World army ant *Eciton burchellii*. *E. burchellii* is considered a top arthropod predator in tropical forests (Franks and Bossert 1983), capturing 30% or more of small leaf-litter arthropods in a 1500 m² area each day (Franks 1982a; Otis et al. 1986; Wrege et al. 2005). *E. burchellii* also plays a significant role in determining spatial distribution of other ant species (Franks and Bossert 1983). *E. burchellii* forage in large, diurnal swarms (Fig. 10) of up to 200,000 individuals (Schneirla 1971). They capture diffusely distributed leaf-
litter insects – primarily *Hymenoptera* species and their larvae – as well as larger arthropod prey items (Franks and Bossert 1983; Otis et al. 1986; Powell and Franks 2005). *E. burchellii* are functionally blind (Schneirla 1971) and have no direct means to assess prey availability, measure swarm foraging success or the overall spatial distribution of ants. They communicate primarily via chemical pheromones left on the substrate, ant-ant contact and the sensing of vibrations (Schneirla 1971).

### Swarming mechanisms in *E. burchellii*

An accurate description of the mechanisms by which *E. burchellii* swarms must provide an explanation for how the ants solve a number of difficult optimization problems, some of which have conflicting goals. First, because their prey is diffusely distributed, they must cover as much area as possible in a day’s raid. However, unlike other *Eciton* species that feed solely on *Hymenoptera*, 50% of *E. burchellii*’s diet consists of large non-*Hymenoptera* prey items which require many ants to capture (Powell and Franks 2005). Consequently, at the local level, *E. burchellii* must have a mechanism to quickly clump when large prey are found while avoiding over-allocation of foragers to any one prey item so gaps are not left elsewhere through which potential prey could escape. Finally, as the swarm passes through an area, it must leave behind it a well-developed trail system over highly heterogeneous substrate. The trail system must permit the efficient movement of thousands of workers an hour to the swarm and facilitate transport of thousands of large prey items to the nest. Development of the trail system provides another conflict within the swarm. Army ants are highly attracted to pheromone (Chapter 2) and appear to continuously leave trail pheromone (personal observation). Yet, in the main part of the swarm, trails are a liability because they can potentially pull workers from being evenly distributed.

### Prey capture

The details of prey capture by *E. burchellii* swarms are almost completely unknown. Although a number of researchers have investigated foraging success rate and prey assemblages (Franks 1982a; Otis et al. 1986; Kaspari and O'Donnell 2003; Wrege et al. 2005) and prey responses to army ant attack (Chadab and Rettenmeyer 1975; Chadab Crepet and Rettenmeyer 1982; Gotwald 1995), to our knowledge, no work has directly examined how *E. burchellii* actually capture their prey.

### Research questions

To examine how *E. burchellii* solve the problems discussed above we analyzed the spatial distribution of ants within a temporal cross-section of an *E. burchellii* swarm. We also measured the probability that a fleeing prey item would encounter an ant as measured by the distance from a random point to the nearest ant. To better understand
prey capture we observed feeding behavior in two captive colonies of *E. burchellii* held at the California Academy of Science museum in San Francisco, California.

**Methods**

In prior work we videotaped foraging *E. burchellii* swarms in the field in Corcovado National Park, Costa Rica (Chapter 2). Swarm video was analyzed by tracking paths of individual ants over time and by measuring head and tail positions of every ant in the frame in every 50th frame in each video clip. We used the ant position dataset from one clip (Chapter 2, clip 1) to create a profile of ant density and of spatial distribution of ants within a swarm.

**Data selection**

Four frames (Fig. 11) were chosen from one of the video clips sampled in our previous work (Chapter 2, “Clip 1”). The four frames were chosen to match four of the distinct areas within the swarm (Fig. 10 and Fig. 11). Frame (1), “early frame” was at the end of the low-density area at the front of the swarm. Frame (2) was the “upstroke,” the start of the main swarm – an area of medium density and the fastest density increase. Frame (3), “peak density,” is in the middle of the swarm at the frame with the highest density observed. Frame (4), “last frame,” was the last video frame recorded. Frame (4) is at the back of the swarm and density is equal to that in frame (2).

**Spatial statistics**

We examined the spatial distribution of ants at four representative times within the swarm using two spatial analysis statistics: “Ripley’s K” and the “empty space statistic,” F(r). Ripley’s K (Ripley 1991) describes the spatial distribution of points (in this case ants) by comparing the observed and expected densities of points within circles of different radii. Ripley’s K indicates whether observed points are more clumped or more evenly spaced than if the points were randomly distributed and at what spatial scales these effects are significant. In this study, observed values that fall below the confidence limits signify that ants are more evenly spaced than would be expected if they were distributed randomly. This indicates that the ants are avoiding each other at these spatial scales. When observed data are above the confidence limits, it indicates that the ants are more clumped at those spatial scales than if they were distributed randomly.
Fig. 11  Temporal profile of ant density in the swarm. Frame (1) – “early frame” corresponds roughly with Fig. 10 area (1); \( N_{\text{ants}} = 60 \). Frame (2) – “upstroke” corresponds with Fig. 10 area (2); \( N_{\text{ants}} = 172 \). Frame (3) – “peak density” corresponds with Fig. 10 area (3); \( N_{\text{ants}} = 325 \). Frame (4) – “last frame” corresponds with Fig. 10 area (4); \( N_{\text{ants}} = 172 \). Inset: Plot of spatial distribution of ants in selected frames.

Because no prey were present in the clip analyzed, we assume that increased clumping indicates that more ants are on trails.

The second spatial statistic, the “empty space function” \( F(r) \), measures the probability a randomly chosen point is within a fixed distance of a point in the dataset (Ripley 1991). In this study, \( F(r) \) provides a measurement of how likely a prey item (i.e., the random point) is to be detected by an ant.

All statistical analyses were performed using the open source statistical package R (Version 2.1.0, http://www.R-project.org) with the spatial statistics library “SpatStat.”

Control distributions

As a control, we generated four sample distributions of points, each with the same number of points as the number of ants observed in the “peak density” frame. Control distributions were as follows: (1) all 321 ants distributed in five, 1 centimeter wide trails
spaced 5 centimeters apart; (2) 30% of the ants randomly distributed off trails; (3) all ants distributed randomly; (4) all ants evenly distributed.

Control distributions were analyzed with the same spatial statistics used on the data. $F(r)$ for the sample distributions provides a measure of how well prey might be detected by ants under four possible spatial distribution strategies. Ripley’s $K$ for the sample distributions provides an indication of how effectively this statistic detects clumping or spacing in known spatial distributions.

### Feeding observations

The two captive *E. burchellii* colonies at the California Academy of Sciences were kept in sealed, 50 m$^2$ enclosures under controlled temperature and humidity. Colonies were fed ~100 g of feed crickets per day in two feedings of about 50 g each. Prior to being fed to the ants, the crickets were placed in a freezer for 5-10 minutes to reduce activity. Because the amount of food the ants were receiving was more than 200% of their normal intake in the wild (Franks 1982a), the ants were not always active prior to feeding times. To initiate swarming prior to feeding periods, small numbers of crickets were dropped on active trails, usually near the bivouac. As ant activity increased, it was usually possible to get the ants to form diffuse swarms. Once the ants were actively searching for food over large areas of the enclosure, crickets were fed to the ants over a 1-3 hour period. In addition to qualitative observations of prey capture, we recorded the time to capture or escape for 48 crickets dropped in areas of medium ant density.

### Results

#### Spatial distribution of ants

A plot of the positions of the ants from the frames analyzed (Fig. 11, inset) provides a snapshot of the spatial distribution of ants in each frame analyzed. Although the ants appear to be randomly distributed in each of the single frames, by contrast, a plot of ants paths over time (Fig. 12) indicates that distinct trails are formed and followed by ants during the swarm.

#### Interaction distance and density avoidance

Ripley’s $K$ analysis of the four frames chosen above indicates that at all times sampled, ants are distributed randomly at most spatial scales (Fig. 13). In our previous work (Chapter 2) we found that density effects begin to impact ant turning behavior when density exceeds ~0.25 ants / cm$^2$. In the three frames where density is higher than this
Fig. 12  Paths of 154 ants throughout the swarm. Paths were chosen at random as ants entered the screen from the top. Ants were tracked until they left the screen or were lost from view (see Chapter 2). Note that despite even sampling of ants, clear paths emerge.

(Fig. 10, (2) – (4), Table 5), Ripley’s K function (Fig. 13, Table 5) indicates that ants begin to avoid each other when they are closer than 7-8 millimeters apart. This result matches the interaction distance of 8 millimeters measured by Couzin and Franks (2003) for ants running on trails. The only frame where Ripley’s K found evidence of clumping (i.e., ants on trails) was the in frame 2, the “upstroke.” In frame 2, the data crosses above the confidence limits at 2.47 centimeters indicating that at spatial scales higher than 2.47 centimeters, the ants are more clumped than they would be if distributed randomly.
Fig. 13  Ripley’s K function for density indicates the spatial distribution of ants as measured by the number of ants found within a circle of radius

Probability of prey detection

The F(r) is an indication of the probability of an ant being within a specific distance of a prey item. Our observations of prey capture in the captive colonies indicated that ants could not detect prey farther than about 2 centimeters away (see (h) below). At this distance, probability a prey item will be detected is high for all densities and 100% at peak densities (Fig. 14, Table 5).
Fig. 14 F(r), the “empty space estimate” function measures the probability (y values) that a prey item at a randomly chosen point will encounter an ant within a given distance (x values). Assuming ants can detect prey within 2 centimeters (see text), we find that a prey item’s probability of detection is 100% in most dense part of the swarm (last four frames and see Table 5).

### Table 5 Summary of results

<table>
<thead>
<tr>
<th>Frame Time (Seconds)</th>
<th>Total ants in frame (Area = 502 cm²)</th>
<th>Ant density per 1 cm²</th>
<th>Max radius of density effects</th>
<th>Prob. of an ant being within 2 cm of point</th>
</tr>
</thead>
<tbody>
<tr>
<td>4551</td>
<td>151.9</td>
<td>60</td>
<td>0.12</td>
<td>--</td>
</tr>
<tr>
<td>5751</td>
<td>191.9</td>
<td>172</td>
<td>0.35</td>
<td>0.81</td>
</tr>
<tr>
<td>6451</td>
<td>215.2</td>
<td>325</td>
<td>0.67</td>
<td>0.73</td>
</tr>
<tr>
<td>7651</td>
<td>255.3</td>
<td>172</td>
<td>0.36</td>
<td>0.72</td>
</tr>
</tbody>
</table>

Analysis of control distributions

Four sample distributions (Fig. 15) were generated using the same number of points as the number of ants observed in the “peak density” frame (Fig. 11; Table 5). Control distributions were analyzed using Ripley’s K (Fig. 16) and F(r) (Fig. 17). Ripley’s K results for the control distributions (Fig. 16) indicates that Ripley’s K successfully picks up the formation of trails as clumping (i.e., the “observed” line is above the confidence limits for a random distribution). Ripley’s K is less effective at
picking up highly even distributions of ants (Fig. 16, (4)). For evenly distributed points, it alternately sees spacing and then clumping depending on the radius being analyzed.

Fig. 15  Four known distributions for comparison. These distributions were generated as a gauge for how the spatial statistics represented known distributions.

F(r) analysis of the control distributions indicates that prey encounter probabilities are much lower when all or most ants are on trails (Fig. 16 (1), (2)). The only sample distribution that has a better chance of prey detection than a random distribution is for perfectly spaced ants (Fig. 17, (4)).

Observations on prey capture

Over a 5-day period, we observed hundreds of ant-cricket interactions in the two captive colonies. The controlled nature of the captive colonies, while clearly artificial, enabled detailed observations of the factors involved in prey capture. Particular attention was paid to factors determining success or failure of prey detection and capture, as well as ant search behaviors and recruitment to prey.

Swarm densities in the captive *E. burchellii* colonies at the California Academy of Sciences were much less than those found in our field samples. Typical swarm density in captive colonies was about 0.12 ants/cm²; swarm density in field measurements ranged
from 0.12 – 0.67 ants / cm² (Fig. 11 and Chapter 2). The captive ants were also less “excited” than is typically observed in wild swarms (see discussion). Even so, results of the “time-to-capture” trials (Fig. 18) indicate that 1 centimeter to medium 3 centimeter sized crickets only have a 20% chance of surviving longer than a minute (N = 48).

A number of factors appeared to have a significant influence on prey capture. First, prey size was important with larger or more active crickets having a much higher chance of escape. Secondly, distribution of ants was very important. The most common
Fig. 16 Ripley’s K analysis of evenness in the control distributions.
Fig. 17  $F(r)$ of the probability of encountering an ant (y values) within a certain distance (x values) for the control distributions. The only distribution that does better than random is a perfectly even distribution.
means of escape for crickets, presumably because orthopterans have very good eyesight (Land 1997), was to avoid detection by moving into gaps where the ants lacked even coverage. When crickets found themselves in areas with no easy gaps in which to hide, they were either captured or forced to jump. If their jump landed them on top of other ants they generally were captured. If they landed in a clear area, they would usually escape.

Once detected by ants, a cricket’s chances of escape seemed primarily dependent on local ant density. If enough ants were around to quickly recruit to the cricket and immobilize it, it would be captured. Ant size also appeared to play a role in capture success. Larger ants seemed better able to grasp the substrate more strongly and thus had a higher chance of preventing prey escape until the arrival of reinforcements.

![Fig. 18](image)

Fig. 18 A cricket’s probability of escaping in an area of medium ant density (~0.12 ants / cm²). Even in areas with ant densities of half those measured in the main swarm, crickets only have a 20% chance of surviving more than a minute.

The first ant to discover a cricket would usually latch onto a limb and hold tightly to the substrate with its tarsal claws (Fig. 19). If other ants were nearby and aware of the cricket, it would be quickly subdued. When there was only one ant near a cricket, capture success appeared to be largely dependent on cricket size, with larger crickets more likely to successfully jump free. Still, individual ants ant frequently managed to hold quite large (>2 centimeter) crickets for extended periods.

**Recruitment and searching for prey**

Generally, ants encountering another ant with prey would immediately attack the prey item. However, some 20-30% of ants would start running swiftly around in a 10 – 30 centimeter radius area, recruiting any other ants contacted. Newly recruited ants would
either attack the cricket or start recruiting as well. It is not clear what caused some ants to recruit and others to attack the prey but it appeared unrelated to number of ants present as sometimes the second ant to arrive at the prey would begin recruitment rather than helping with prey capture.

Overall, two types of recruitment behavior were observed. Most frequently, recruitment was “indirect,” as described above – an ant contacting prey would run swiftly with high turn frequency, in a 10 - 30 centimeter radius area. When the recruiter encountered other ants, they would begin similar behavior. The increased speed and turn angle of recruited ants usually brought them quickly into contact with the prey item.

“Direct” recruitment, where an ant ran to a nearby trail and returned directly to the prey with multiple workers was far less common.

If the cricket escaped at any point, all ants involved would immediately begin to swiftly search the area; any other ants encountered would also be recruited to searching. This agitated searching behavior generally continued for 30 to 60 seconds after which the ant(s) would gradually return to behaving as they had been prior to prey contact.

There was no obvious difference between indirect recruitment and searching behavior resulting from prey escape. Other ants contacted by a searching or a recruiting ant generally exhibited similar fast running and turning behavior and “agitation.” In both recruiting and searching for prey, neither the location of the lost prey or of other ants is
known by the searching ant(s). Thus is it possible that there is no behavioral difference these two responses.

Recruitment pheromones

In hundreds of observations of prey capture we found no evidence that *E. burchellii* uses any sort of fast-acting volatile chemical for worker recruitment to prey as has been found in other army ants (Chadab and Rettenmeyer 1975; Topoff et al. 1980; Witte and Maschwitz 2002). Ants almost never (< 5%) responded to a prey item or ant if they were farther away than 2 centimeters In four isolation experiments where a single ant holding a cricket was surrounded with a thin wire mesh, even ants walking directly on the other side of the mesh (i.e., < 1 millimeter away) showed no reaction to the ant with the prey item.

Discussion

Overview

Successful foraging in *Eciton burchellii* requires a high degree of efficiency for a number of reasons. First, foraging is energetically costly and time limited (Burton and Franks 1985; Bartholomew et al. 1988; Feener et al. 1988; Partridge et al. 1996; Franks et al. 1999; Boswell et al. 2001; Powell and Franks 2005; Wrege et al. 2005). Secondly, many of the large prey items on which *E. burchellii* specializes have good eyesight (Land 1997; Land and Nilsson 2002) and many can jump 1-2 meters. Finally, *E. burchellii* is attended by a host of obligate and opportunistic antbirds that parasitize about 15% of a colony’s daily intake (Wrege et al. 2005). To overcome these challenges, *E. burchellii* swarms much move swiftly while maintaining even coverage, high local densities, and sufficient swarm width and depth that jumping prey are likely to be caught when they land. Swarm width is also important because it determines the overall amount of area searched in a day. Our previous work (Chapter 2) found that *E. burchellii* foraging swarms are primarily organized by three factors: ant reaction to the pheromone landscape, avoidance of high density areas and variation in running speed due to ant length. We showed that longer ants are disproportionately represented at the front of the swarm where they are able to search the area more quickly than shorter ants.

In our previous work, we hypothesized that capture success is largely dependent on the ants evenly distributing themselves while maintaining roughly standard densities in the main part of the swarm. Yet, we also found that ants are strongly attracted to pheromone trails (Chapter 2) and that clear trails develop early on as the swarm moves through an area (Fig. 12; Chapter 2). The results of our current work show that the ants manage to both lay an effective trail system and maintain an even distribution in space using only a few simple mechanisms.

Spatial distribution and density avoidance

Analysis of the spatial distributions of ants over time from (Fig. 11, inset, Fig. 13) indicates that the ants distribute themselves in space as evenly as if they had intentionally
sought a random distribution. The primary mechanism enabling such even distributions appears to be density avoidance. The density effects observed in our previous work (Chapter 2) begin to emerge as overall densities exceed 0.25 ants/centimeter$^2$ (Chapter 2). Ripley’s K analysis of the spatial clumping of the ants for the three frames with densities higher than this value (Fig. 13 (2) – (4)) show that ants start to avoid each other when within 7-8 millimeters of each other.

It is interesting that despite the clear emergence of paths (Fig. 12 and Chapter 2), ant distribution in individual frames (Fig. 11, inset) and spatial analysis of this distribution (Fig. 13, Table 5) show that from the point of view of prey, ants are in a random distribution at almost all spatial scales and times.

Observations of pioneer ants in swarm videos indicate that ants can detect a “path” laid by only one or two previous ants. When tracking pioneer ants in the video clips, it was often observed (T. Brown) that pioneers would follow the trail of a previous pioneer for a while before losing it again. However, this occasional trail following behavior is swamped by the fact that few ants are present and they are arriving in a more or less even distribution. Consequently, the overall behavior of the pioneers is random searching of an area. It should be noted that the width of the low ant density area searched by pioneers at the front of the swarm is as wide or wider than the swarm itself, and that the transition from very few ants to very dense ants happens very rapidly and over a short distance (Fig. 11 and Chapter 2). This means that the pioneers search an area for 1-2 minutes, laying down the first network of trails. The ants arriving behind the pioneers end up, to some degree, on these trails. This early tendency to be on emergent trails is visible in the “upstroke” frame where Ripley’s K shows clumping at spatial scales above 2.4 centimeters. However, rapid density increases soon force arriving ants off the trails and they begin filling the space available. Thus, although trails exist and are being followed by the ants that are on them, there is little clumping in the main swarm because of density effects. As density lessens towards the back of the swarm, one sees that clear trials of ants begin to emerge (e.g., Fig. 10). Unfortunately, none of our video clips was recorded long enough to capture this transition at the back of the swarm from high ant density to all ants being on trails. One would expect Ripley’s K analysis of frames in later portions of the swarm to match those in the sample distributions of ants on trails (Fig. 11, Fig. 16 (1) and (2)).

Likelihood of prey detection

Results of the F(r) “empty space” analysis indicate that at peak densities, a prey item has a 90% chance of being detected within 1 centimeter (Fig. 14, Table 5). Even at quite low densities such as those found early in the swarm, prey items still have a 30% chance of being detected. In addition, it should be noted that the F(r) analysis only looks at the distance from a single point to the nearest ant, whereas large prey items are often many centimeters long. Probability of detection at distances above 2 centimeters is close to 100% for every point in the main swarm. Even in the first frame, where density is low, probability of detection reaches 100% by 3 centimeters.
Prey capture in *E. burchellii*

Our results indicate that large prey stands little chance of escaping if they are detected by enough ants to capture them. However, if detected prey is to be captured, there must be enough ants around to do so. The results of our observations on prey capture provide another reason why it may be optimal for longer ants to be pioneers – they may be better able to capture and hold larger prey until the rest of the swarm arrives.

As noted earlier, the captive colonies observed in the prey capture experiments were being fed more than twice what a normal colony would eat in a day. As a result, the role of ant excitement in foraging became quite clear. When the ants were not foraging, they were highly attracted to pheromone and would rarely leave well laid-in trails. In addition, they were much less reactive to prey when they were not actively foraging. The result was that the colonies foraged weakly, and in much smaller numbers than is commonly observed in the wild. It is well known that when *E. burchellii* colonies are nomadic and the ants have thousands of larvae to feed, the swarms are much more intense, go farther and last longer (Schneirla 1971). This observation fits in well with the results of our work. Because all of the processes organizing the swarm are self-organized, all of these observed responses – longer foraging days, larger, more intense and faster moving swarms – emerge from the simple response of hungrier ants performing the same tasks at a higher level of excitement.

The impact of excitement on behavior also provides a possible explanation for how the ants avoid over-recruitment to prey items. Initiation of prey capture is generally believed to be the result of the ants reacting to movement by the prey item. In fact many potential prey avoid capture by standing completely still (Schneirla 1971). Our observations suggest that a similar mechanism mediate recruitment to prey. When few ants are on a prey item, its convulsions roll the ball of ants and prey around picking up other ants and recruiting ants from afar. As sufficient ants have covered the prey and it begins to die, movement is reduced until it no longer acts as an attractive element in the landscape.

Conclusions

As noted earlier, much of *E. burchellii* larger prey items have good eyesight and so it is essential that, as much as possible, ants take large prey by surprise. In both clips examined, ant densities increase 2-3 fold in less under 30 seconds (Fig. 11 and Chapter 2). Thus the swift increase in density at the swarm front, in addition to helping maintain even densities (Chapter 2) also has another purpose – it allows *E. burchellii* to quickly overwhelm large, highly mobile prey items. In addition, since antbirds have been shown to take prey items that the ants do not immediately subdue and cover with ants (Wrege et al. 2005), quick prey capture helps the ants reduce parasitism.

The simple rules described in this and the previous chapter, enable *E. burchellii* to attain a high level of capture success with large prey items as well as to harvest significant percentage of small leaf litter arthropods. Without any means to globally share information, *E. burchellii* does an excellent job of filling in space and maintaining even
densities as well as building and maintaining an extensive trails system to support the swarm. As a result, it effectively exploits its specific niche in the forest.
CHAPTER 4

MODELING THE EMERGENCE OF COMPLEX BEHAVIORS FROM SIMPLE RULES. A SELF-ORGANIZED MODEL OF ARMY ANT SWARMING

Abstract

Complex self-organized foraging swarms of the New World army ant *E. burchellii* are organized, to a large degree, through simple rules. We present the results of an individual-based model of army ant swarming in continuous space. The model incorporates individual response to pheromone and density and is parameterized almost exclusively with data measured from video of army ant swarms. The model exhibits high congruence with quantitative descriptions of swarming patterns measured in our previous work. Our results provide strong support for the utility of a data-driven approach to understanding self-organized processes that combines computer modeling with rigorous empirical work.

Introduction

A primary goal of self-organization research is to understand the processes by which complex behavioral patterns emerge from interactions between relatively simple individual components in living systems. The organizational structure of social insect colonies makes them a particularly useful system for modelers interested in better understanding how self-organized processes work. In social insects, it is possible to directly measure individual behaviors such as foraging and simultaneously, to observe the impact these choices have on colony fitness. Few other living systems are as well suited for this type of work.

The highly organized swarms of *Eciton burchellii* army ants are an ideal social insect system for studying self-organization. *E. burchellii* foraging is computationally complex, but as individuals, *E. burchellii* are relatively behaviorally simple, almost blind (Schneirla 1940; Schneirla 1971) and only have access to limited local information about the state of the swarm. In army ants, self-organization provides a mechanism by which changes in simple individual behaviors such as velocity or turn angle, in response to variations in pheromone concentration or local ant density, can, when summed over the whole swarm, generate effective group foraging decisions.

*E. burchellii* foraging is under considerable time and energetic constraints (Burton and Franks 1985; Bartholomew et al. 1988; Feener et al. 1988; Partridge et al. 1996; Franks et al. 1999; Boswell et al. 2001; Powell and Franks 2005; Wrege et al. 2005). To forage effectively, colonies must distribute some 200,000 nearly blind individuals to search an area of about 1,500 m² in a 12 – 14 hour day (Schneirla 1971; Franks 1982a; Swartz 1997). During this time, the ants can capture, process and retrieve some 30,000 prey items (Franks 1982b). Swarms generally progress at 14 – 18 meters per hour,
densely covering a 10 by 4 meter area with ants (Schneirla 1940; Swartz 1997, Chapter 2). The densest part of the swarm front is typically a few meters deep with a fan stretching back 5 or more meters. E. burchellii can form functional swarms with a few thousand to a few hundred thousand individuals (personal observation).

Capture success in E. burchellii is largely dependent on the ants maintaining relatively even distributions in all areas of the swarm while covering as much area as possible (Chapter 3). However, the ants can only measure current density from their immediate environment and an approximation of past ant densities from the local pheromone landscape they perceive. We demonstrated in Chapter 3 that these self-organizing mechanisms in E. burchellii swarms enable the ants to distribute themselves as well as if they had intentionally sought a random distribution. The ants thus effectively search an area completely as they move through it, providing opportunities for high levels of capture success. Our previous work suggested that the ants are able to do this almost solely through modification of their turning behavior in response to differing pheromone levels and to local ant density. Ant size also appears to play an important role in swarm organization, with longer ants running faster and thus being over-represented as “pioneers” at the front of the swarm.

The modeling approach

Studying self-organized systems presents particular challenge for modelers. Collecting enough data to accurately describe the essential features of complex systems is often very difficult. What makes a system self-organized is, by definition, the appearance of properties at the system level that cannot be predicted by a simple description of the parts (Camazine 2001). Models that have real biological utility are able to distill essential features from a system while maintaining enough of the original complexity to provide biologically useful results. Large strides have been made in this area in recent years (e.g., Camazine 2001; Solé and Bascompte 2006).

Previous swarm models

General models of ant swarms are fairly numerous in the literature (Deneubourg et al. 1989; Franks et al. 1991; Millonas 1992; Chialvo and Millonas 1995; Watmough and Edelstein Keshet 1995; Solé et al. 2000). However, the primary goal of most of these models has been to qualitatively examine pattern formation and self-organization in artificial swarms. Some of these models successfully generated a visual approximation of army ant swarm patterns (Deneubourg et al. 1989; Franks et al. 1991). However, all previous models have been hampered by the lack of quantitative data on army ant swarms. Consequently, most essential parameters of these models such as turning response rates to pheromone were taken from other ant systems. Yet pheromone systems, trail-running behavior, foraging strategies and prey distribution vary widely across ant genera and even between closely related army ant species (Chadab and Rettenmeyer 1975; Witte and Maschwitz 2000; Witte and Maschwitz 2002). In addition, the swarming patterns characteristic of different army ant species seem to be highly dependent on specific relations between the above factors (Deneubourg et al. 1989; Franks et al. 1991;
Camazine 2001). The above issues suggest that if modelers seek to explore the actual processes underlying self-organized behaviors specific ant species and particularly in army ants, it is essential that they use parameters measured from the system of interest and have a quantitative dataset with which to compare model outputs. Yet, very little is known about the actual organization and internal dynamics of army ant swarms and until our current work, model outputs could not be compared to quantitative descriptions of swarming behavior because such descriptions did not exist.

Initial modeling work on *E. burchellii* swarming by Deneubourg et al. (DEN) (2003) showed that simple rules about how army ants responded to pheromone could generate patterns that were visually similar to real swarm patterns. Parameter values used by DEN are summarized below and in Table 6a. The DEN model was based on the following assumptions, matching what was then known about army ant foraging:

**Movement and running velocity**

The probability an ant will move is based on the concentration of pheromone at the two nodes in front of it. Increase in velocity due to pheromone stems from an increase in the probability of ant movement such that an ant runs at 50% of peak velocity when pheromone values are equivalent to the passage of 40 ants.

**Pheromone**

At each step, ants leave 1 unit of pheromone. Once an ant has made the decision to move, it chooses which branch to follow based on which node in front of it has higher pheromone, subject to an error term. Mean life of trail pheromone is 2 minutes.

**Density effects**

Each node in the simulation represents 25 square centimeters. Nodes are 5 centimeters apart. Only 5 ants can occupy a given node at one time (i.e., 1 ant / 5 cm²). Ants will move to the adjacent node if the node they want to move to is full.

The DEN model demonstrated that simple behavioral rules could generate patterns which visually approximate those observed in the real world. In addition, they showed that significantly different swarming patterns, which approximated those of two different army ant species, could be generated by only varying prey distribution rather than changing the behavioral rule set.

Our empirical work (Chapter 2) has shown that the assumptions of the DEN model fail to accurately reflect the behavior of *E. burchellii* in a number of important ways. First, we found that ants at the front of the swarm run faster in areas where few ants have been (i.e., low pheromone areas). Consequently, a different mechanism is needed to regulate velocity. In addition, both our work (Chapter 2) and Couzin and Franks’ (Couzin and Franks 2003) found that density interactions strongly affect turning behavior and that ants actively update body angle and velocity based on the behavior of their neighbors. Although the DEN model incorporated spatial density, in that only one ant was permitted per 5 cm², it did not examine the direct influence that density has on turning behavior and velocity.
Recent modeling work on trail formation in *E. burchellii* by Couzin and Franks (Schneirla 1971) incorporated direct measurements of ant-ant reaction distances and turning behaviors measured from video recordings of army ant trail systems. In their model, ant reactions to approaching neighbors played a determining role in shaping individual trajectories and in lane formation. However, their model did not address swarming behavior, and the pheromone landscape experienced by the ants was fixed. Parameter values used in the Couzin and Franks model are summarized in Table 6b.

### Table 6 Parameter values for previous army ant models.

#### a Parameter values for Deneubourg et al. (1989)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grid shape</td>
<td>Diamond</td>
</tr>
<tr>
<td>Size of grid point</td>
<td>25 cm²</td>
</tr>
<tr>
<td>Distance between grid points</td>
<td>5 cm</td>
</tr>
<tr>
<td>Pheromone deposited per step</td>
<td></td>
</tr>
<tr>
<td>Concentration of pheromone with</td>
<td></td>
</tr>
<tr>
<td>50% probability of movement</td>
<td>40</td>
</tr>
<tr>
<td>Mean lifetime of pheromone</td>
<td>2 minutes</td>
</tr>
<tr>
<td>Probability of encountering 1 unit of prey</td>
<td>50%</td>
</tr>
<tr>
<td>Ant leaving nest per second</td>
<td>2 – 10</td>
</tr>
<tr>
<td>Time step</td>
<td>4 seconds</td>
</tr>
<tr>
<td>Cut-off for leaving pheromone</td>
<td></td>
</tr>
<tr>
<td>Outbound: 1000</td>
<td></td>
</tr>
<tr>
<td>Inbound: 300</td>
<td></td>
</tr>
</tbody>
</table>

#### b Parameter values for Couzin and Franks (2003)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial scale</td>
<td>–</td>
<td>Continuous torus</td>
</tr>
<tr>
<td>Pheromone</td>
<td>–</td>
<td>Fixed Pre-set trail with fixed concentration profile</td>
</tr>
<tr>
<td>Body length</td>
<td>β</td>
<td>0.8 cm</td>
</tr>
<tr>
<td>Antenna length</td>
<td>φ</td>
<td>0.4 cm</td>
</tr>
<tr>
<td>Radius of body perception circle</td>
<td>r_d</td>
<td>0.4 cm</td>
</tr>
<tr>
<td>Radius of forward perception circle</td>
<td>r_p</td>
<td>1.2 cm</td>
</tr>
<tr>
<td>Acceleration / deceleration rate</td>
<td>μ / -μ</td>
<td>50 cm / sec²</td>
</tr>
<tr>
<td>Minimum Speed</td>
<td>u_min</td>
<td>2 cm / sec</td>
</tr>
<tr>
<td>Maximum (desired) speed</td>
<td>u_max</td>
<td>13 cm / sec</td>
</tr>
<tr>
<td>Internal angle of ant’s forward perception field</td>
<td>α</td>
<td>90°</td>
</tr>
<tr>
<td>Rate at which ant turns away from others.</td>
<td>θ_p</td>
<td>500°/ sec Range: 100-900</td>
</tr>
<tr>
<td>Time step</td>
<td>t</td>
<td>0.02 sec</td>
</tr>
<tr>
<td>The most an ant can turn in one time step.</td>
<td>θ_pΔt</td>
<td>10° if θ_p = 500</td>
</tr>
<tr>
<td>Turn error Gaussian-distributed random deviate centered on 0 with SD = σ.</td>
<td>σ</td>
<td>0.01 – 1.0</td>
</tr>
<tr>
<td>Amount of pheromone deposited</td>
<td>Q</td>
<td>$1.2 \times 10^{-6}$ g/ cm³</td>
</tr>
</tbody>
</table>
Research questions

In our previous work (Chapter 2, 3) we argued that we had successfully described the primary mechanisms involved in producing swarm behavior in *E. burchelli*. To test the accuracy of our empirical results we built an individual based model of *E. burchelli* swarming. Model parameters were almost all measured directly from video of army ant swarms. Matching model outputs were compared quantitatively with results measured from swarms in the field (Chapter 2, 3). In addition to permitting investigation of our earlier results, the model enables us to more closely examine the relative importance of the factors believed to influence swarming behavior and to generate predictions that can be tested in the field.

Our primary questions were:

1) Are the ant pheromone response and ant-ant interaction responses measured in Chapter’s 2 and 3 sufficient to generate the characteristic swarm patterns measured in real swarms?

2) Does the swarm move forward at characteristic velocities that are slower than that of individual ants?

3) Is the spatial distribution of ants by size similar to that found in real swarms?

Methods

Data collection from *E. burchelli* swarms

*Eciton burchelli* army ant swarms were filmed with a Sony single-chip digital video camera near Sirena Research Station, Corcovado National Park, Costa Rica. Data collection and analysis of swarm data is described in detail in Chapters 2 and 3. Results of our analysis provide a profile of ant density, body and turn angles, velocities, and paths within a temporal cross-section of a swarm. An approximate map of the pheromone landscape experienced by the ants was created, allowing us to measure how ant turning behavior changes in response to relative amount of pheromone experienced. These data will be collectively referred to as “video data.”

Model parameterization

An individual-based model of army ant swarming was developed using the parameters estimated in Chapters 2 and 3 and as described below. The model was created using the Matlab software package (MathWorks, 2006a).

Model time step

Model time step (\(\Delta t\)) was set to 1/30 second to match the frame rate of the video data. Ant behaviors are processed in parallel in each time step.
Area size and shape

The ants move on a continuous world which is 20 centimeters wide and 10 meters long with wrapping boundaries on the sides and top and a reflecting boundary on the bottom. The height of the model was chosen as slightly longer than the expected travel distance of the swarm over the 4-minute runtimes of the model. The reduced width of the world was a computational necessity. Because army ants frequently swarm effectively up tall trees, a tall, circular object is a biologically reasonable shape for the ants to explore (Topoff and Mirenda 1975).

Initial body position and body angle

All ants are given the same initial vertical position near the bottom of the screen and a random horizontal position. All ants are given an initial random body angle with mean of 0 (pointing straight up) and standard deviation of $\pi/8$.

Ant number

Our calculations suggest that 2,000 – 7,000 individual ants passed through the area measured in the video clips in the timescale in which we sampled. Model runs were performed with 2000 ants due to computational constraints.

Ant lengths and velocity

All ants have the same length, 5.4 millimeters, the mean length of ants measured in the two video clips analyzed ($N = 19,585$ ants). The only factor consistently determined by length in our analysis of the video data was running speed. Behavioral variation due to length was modeled by assigning the ants a range of maximum velocities in a Gaussian normal distribution matching the mean velocities observed in the video clips ($v_{\text{max}} = 3.8 \text{ cm/ sec}; \sigma = 0.98$). An ant will run at its maximum velocity, $v_{\text{max}}$, unless it is slowed by an interaction with another ant (equation 2.2).

Release rate

In each trial run, the ants were arbitrarily given a start time such that the average departure rate of ants was equal to the release rate ($R$). Release rates were based on our observations of arrival rate of ants on the screen in the data clips and measurement rate of departure for ants leaving the nest during initiation of swarming (T. Brown, unpublished data). Default value for $R$ was 30 ants/sec.

Effects of pheromone on ant velocity

Velocity reductions observed in our data in areas of intermediate pheromone values were assumed to result primarily from density interactions (Chapter 2). Pheromone effects on ant velocity were not modeled explicitly.

Mapping the pheromone landscape in field recorded video of army ant swarms
Obtaining an exact map of the pheromone landscape experienced by the videotaped ants would require knowing pheromone deposition rates by E. burchellii and the actual number of ants passing each point. However, it is currently not technically feasible to track the positions of all ants in a swarm and pheromone deposition rate is unknown. To map the approximate pheromone landscape experienced by the ants in the videos, we counted cumulative number of ants passing each point on a 2 millimeter-scale grid every 50 video frames (clip lengths were 6,051 and 7,651 frames). Pheromone deposition was assumed to be one unit pheromone per ant per step under all circumstances. The resulting “pheromone” landscape was smoothed every 10 video frames to approximate the lateral diffusion of pheromone on the substrate. Further empirical work is needed to determine if the accuracy of our assumptions about pheromone deposition and diffusion. However, we believe it is a reasonable starting point for two reasons. First, observations of video taken at ground-level of army ants running on flat substrate and branches suggest that E. burchellii continuously exhibits high gaster-touch rates in all parts of the swarm (i.e., pioneers, main swarm, ants on trails, etc). Second, the high velocity of ants (2 millimeters or more per 1/30 second) would require that the ants leave pheromone on this timescale in order for a continuous trail to emerge.

Derivation of turn response to pheromone

Ant body angles were matched with the estimated pheromone values under each antennae at the ant’s previous position for each step in an ant’s path. Using these data, we derived the pheromone response equation using a linear mixed effects model fitted to ant turning response to pheromone present in relation to the difference of pheromone between antennae, and total pheromone present (2 clips, N = 18,993 samples, 154 paths, $p < 2 \times 10^{-16}$).

Derivation of model turn algorithm (equation 2.1)

In the video data, the pheromone landscape from which the turn equation was derived was based on a subsampling of the total number of ants passing under the camera. However, because the model records all ants leaving pheromone, not just a subset, the turn equation used in the model must be scaled by the actual number of ants that passed by each point in the dataset. The strength of pheromone response ($\gamma$) can be estimated by multiplying the sample rate by the total number of ants observed. This calculation indicates that the measured turning response should be scaled by about 1/18 (Table 7).
Table 7  Calculation of pheromone response strength scalar (γ).

<table>
<thead>
<tr>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total ants sampled</td>
<td>19,585</td>
</tr>
<tr>
<td>Scaled number of ants in both clips</td>
<td>(19,585 * 50) = 979,250*</td>
</tr>
<tr>
<td>Total ants positions used to generate pheromone map</td>
<td>55,364</td>
</tr>
<tr>
<td>Scaled value of a measured “unit” of pheromone</td>
<td>979,250</td>
</tr>
<tr>
<td></td>
<td>55,364</td>
</tr>
</tbody>
</table>

* This number is substantially larger than the actual number of ants present because it records a position for every ant in every frame in which the ant is visible on the screen.

Pheromone in model and ant turning response to pheromone

Ants in the model deposit one unit of pheromone at every step (1/30th second). To mimic diffusion of pheromone in the air and on the landscape, each unit of pheromone is thinly spread over a 5 mm² area at the time it is deposited. Pheromone values over the 5 mm² area were calculated using the same smoothing algorithm used in analyzing the video data analysis (Chapter 2). The spreading of pheromone approximates the fact that pheromone is volatile in the environment and that army ants can sense trail pheromone in the air (Torgerson and Akre 1970b; Franks et al. 1991).

At the start of every time step, the amount each ant turns (θ) is determined by the amount of pheromone it senses under each antenna, based on equation 2.1 (Table 8), of the residuals from the fit of turning response to pheromone in the ant path data from Chapter 2. Initial model runs using the full variance yielded chaotic results because the random component of each turn exceeded the ants’ maximal turn angle in response to pheromone. Real army ants react to many biotic factors not measured in our data and they are moving over a complex and highly heterogeneous substrate. The residuals in the

| Table 8  Equations used in current model                                                                 |
|-----------------|---------------------------------------------|
| Equation Number | Description                                 | Equation                                                                 |
| 2.1             | Turning response to pheromone               | \[ \theta = \gamma \times -0.13898 \times \Delta Q \times (\gamma^2 \times 0.01762 \times \Delta Q \times Q) + \varepsilon \] |
| 2.2             | Velocity reduction via density interaction  | \[ v_t = v_{t-1} \left( \frac{1 + \bar{c}_1(t) \cdot \bar{c}_1(t)}{2} \right)^{0.25} \] |
| 2.3             | New position vector of ant (\( \bar{c}_1 \)) | \[ \bar{c}_1(t+\Delta t) = \ell \times \frac{\bar{c}_1(t) + \bar{c}_2(t) \times \tau}{\| \bar{c}_1(t) + \bar{c}_2(t) \times \tau \|} \] |
| 2.4             | Ant acceleration                            | \[ v_{t+1} = \alpha \times v + (1 - \alpha) \times v_{\text{max}} \] |
model fit capture all of these sources of variation whereas we are only interesting in
the component of this variation associated with turning response to pheromone.

Density interactions

After an ant has turned as described in the previous section, it looks to see if there
is another ant in the box closest to the limit of its perception distance \( r_d \). Based on the
values of ant-ant perception distance used by Couzin and Franks (2003) and our
measurements (Chapter 3), ant positions for density interactions are tracked on an 8
millimeter grid. For computational simplicity, only one ant is recorded per grid space for
density interactions. Thus, where density is concerned, an ant looking at a given grid
space can see only one other ant at that location no matter how many ants may be there.
This assumption is reasonable for two reasons. First, we have no evidence that an ant
perceiving one ant in its way behaves differently than an ant perceiving two ants.
Secondly, analysis of video of dense swarms suggests that there is rarely more than
1 ant/cm\(^2\). The outcome of recording single ants in the density grid is that ants react
normally to density by slowing and turning but there is no inherent limit on the number of
ants present in a given grid area.

If an ant finds another ant in the position where it is looking, the following
interactions occur:

1) Both ants slow by an amount \( \Delta v \), Table 8, eq. 2.2). \( \Delta v \) scales such that ant
velocity is reduced to 0 in head-to-head interactions and unaffected if body
positions are parallel. Velocity reduction takes place sequentially, first for the
ants that are seen and then for the ants that see another ant. If an ant is both
seen by an ant and sees another ant, its velocity is reduced twice.

2) The current ant updates the angle of its position vector \( \vec{c}_1(t) \) based on an
average of its current position and the body position of the ant it sees \( \vec{c}_2 \). The
strength of this interaction is determined by the density scalar \( \tau \) or
“contact alignment” which determines how many steps it takes for two ants to
match body angles. The ant’s new body angle \( \vec{c}_1(t + \Delta t) \) is then calculated
from its new position vector (Eq. 2.3).

3) After the ants move, each ant registers its position at the nearest point in the
density grid. Although all ant movements are processed in parallel, when there
are multiple ants in one box, the last ant in the table of ants is the ant
registered.

4) Prior to the next time step, all ants accelerate towards their maximum velocity
\( v_{\text{max}} \) based on the acceleration constant \( \alpha \), Eq. 2.4). At default values for \( \alpha \n(\text{Table 9}) \) it takes about ½ second for an ant to regain its maximum velocity
after an interaction.

Movement and pheromone

After all ants have turned and adjusted their velocity due to density interactions,
each ant’s midpoint is moved a distance \( \Delta(x,y) \) in the direction each ant is pointed, based
on its velocity. Positions of all parts of the ant (head, tail and antenna) are then calculated based on the ant’s new body angle and position. After each ant has turned and moved it leaves a drop of pheromone at its new tail position. Ant position is recorded as a continuous variable; pheromone concentration is recorded on a 1 millimeter scale. To mimic the effects of pheromone diffusion in the air and over substrate, each unit of pheromone is spread in a bivariate normal distribution over a 5 millimeter area at the time it is left (Table 9). The half-life of *E. burchelli* trail pheromone has been estimated at

Table 9  Model parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Baseline Value (Variations tested)</th>
<th>Range examined</th>
<th>Source of parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>General model parameters</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total run time</td>
<td></td>
<td>240 seconds</td>
<td>1 – 20 min.</td>
<td>–</td>
</tr>
<tr>
<td>Model time step</td>
<td>t</td>
<td>1/30 second</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Arena width</td>
<td></td>
<td>20 cm</td>
<td>20 cm – 5 m</td>
<td>–</td>
</tr>
<tr>
<td>World height</td>
<td></td>
<td>10 meters</td>
<td>1 – 20 m</td>
<td>–</td>
</tr>
<tr>
<td>Total ants</td>
<td></td>
<td>2000</td>
<td>500 - 6000</td>
<td>Measured</td>
</tr>
<tr>
<td>Initial horizontal spread of ants</td>
<td></td>
<td>5 cm</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Release rate</td>
<td>R</td>
<td>30 ants per second (15; 50)</td>
<td>10 - 60</td>
<td>Measured</td>
</tr>
<tr>
<td>Ant length</td>
<td>l</td>
<td>5 mm</td>
<td>2 –12 mm</td>
<td>Measured</td>
</tr>
<tr>
<td>Antennae length</td>
<td></td>
<td>4 mm</td>
<td>–</td>
<td>Couzin and Franks (2003)</td>
</tr>
<tr>
<td><strong>Density Interactions</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scale of density grid</td>
<td></td>
<td>8 mm</td>
<td>5 – 10 mm</td>
<td>Smallest computationally feasible value</td>
</tr>
<tr>
<td>Perception distance for density interactions</td>
<td>r_d</td>
<td>8 mm</td>
<td>5 – 10 mm</td>
<td>Measured</td>
</tr>
<tr>
<td>Density response scalar</td>
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<td>1 – 0.05</td>
<td>Video observations</td>
</tr>
<tr>
<td>Acceleration constant</td>
<td>α</td>
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<td>0.5 – 0.98</td>
<td>Video observations</td>
</tr>
<tr>
<td><strong>Pheromone</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Strength of</td>
<td>γ</td>
<td>0.056</td>
<td>1 – 0.025</td>
<td>Measured</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>------------------------------</td>
<td>------------------</td>
<td>------------------</td>
<td>------------------</td>
<td></td>
</tr>
<tr>
<td>pheromone response</td>
<td>(0.025; 0.1)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pheromone dropped per step</td>
<td>$\rho$</td>
<td>1 unit</td>
<td>Estimated</td>
<td></td>
</tr>
<tr>
<td>Width of a pheromone drop</td>
<td>5 mm</td>
<td>1 – 10 mm</td>
<td>Estimated</td>
<td></td>
</tr>
<tr>
<td>Error in pheromone response</td>
<td>$\varepsilon$</td>
<td>Gaussian distributed, $\sigma = 0.058$ (0; 0.116)</td>
<td>0 – 0.2</td>
<td>Measured</td>
</tr>
<tr>
<td>Velocity</td>
<td>$\nu$</td>
<td>Mean = 3.8 cm / sec $\sigma = 0.98$; $\sigma = 0–2$</td>
<td>Measured</td>
<td></td>
</tr>
<tr>
<td>Difference in pheromone</td>
<td>$\Delta Q$</td>
<td></td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>between left and right</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>antennae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total pheromone both under</td>
<td>$Q$</td>
<td></td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>antennae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Value of pheromone dropped</td>
<td>6.963e-8 2.809e-5 2.076e-4 2.809e-5 6.963e-8</td>
<td>2.809e-5 0.0113 0.0837 0.0113 2.809e-5</td>
<td>2.076e-4 0.0837 0.619 0.0837 2.076e-4</td>
<td>2.809e-5 0.0113 0.0837 0.0113 2.809e-5</td>
</tr>
<tr>
<td>over 5x5 mm area</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
about 132 minutes, so the effects of evaporation need not be considered on the

Model runs, outputs and data collection

Twenty model runs were performed with the baseline parameters listed in
Table 9. Twenty additional trials were performed for each of parameter variations listed
in Table 9. All model runs had 2,000 ants and lasted 4 minutes. For each model run, a
visual map of the ants was recorded at each second to generate a movie of swarm
behavior. The following parameters were recorded every 10 seconds in each model run:

1) Density, spatial distribution and body angles of all of ants.
2) Shape and velocity of swarm front.
3) Spatial distributions of ants by “length” as measured by an ants maximum
   velocity ($v_{\text{max}}$).
4) A visual map of pheromone distribution.

Model output analysis

All model outputs were analyzed using the Matlab software package with
methods similar to those described in Chapter 2. All statistical analyses were performed
using the open source statistical package R (Version 2.4.0, www.R-project.org). All
results presented below are the means of data from four frames in each simulation
($T = 150, 180, 210$ and $240$ seconds). Means from each trial were then averaged across
all twenty model runs for each parameter variation to generate the values presented in
Table 10 and Fig. 20 - Fig. 25). Differences between parameter variations were calculated
using the Tukey ‘s Honest Significant Difference' measure in R.

Because standard deviation does not provide an accurate measure of cohesion for
angles, we examined cohesion of ant body angles using “mean circular dispersion”
(Schneirla 1971) as in Chapter 2. MCD ranges from 0 to 1 with lower values indicating
higher congruence of angles in the sample. For the video and model data, MCD of all the
ants in an area provides a measure of the degree of density-dependent coherence. In the
video data, MCD was taken at each frame where density was sampled. The slope of the
line fitted to these values provides a profile of body angle cohesion throughout a temporal
cross-section of the swarm (Chapter 2, Fig. 4). In the model, unlike in the video data, the
body angle and position of all ants is known at all times. To match the sampling method
used in the data, at each time when swarm data was recorded we broke the swarm data
into adjacent vertical slices with area matching the area sampled in the video data. The
slope of the line through these data points provides a measure of density-dependent
coherence within the swarm front.

The extent of the swarm front was determined as the area where standard
deviation of ant vertical position was greater than 4 centimeters and ant density was
greater than 1 ant / 10 cm².
Results

Parameters tested

Parameter variations tested are described in Table 9. All results described below are presented numerically in Table 10. Swarm maps and density and MCD profiles of the baseline and each model variation are presented in Fig. 20 and Fig. 21 (baseline) and Fig. 26 to Fig. 37 (variations). Comparisons of effects on output measures between model variations and the baseline are presented in Fig. 22 to Fig. 25. All distances are in centimeters.

Model output with baseline values

Model runs using the baseline values show clear formation of foraging trails and a well-delineated swarm front (Fig. 20). In the baseline model runs, ant densities within the swarm are significantly higher than those measured in the video data. Swarm depths are similar to the depth of the swarm in clip 2. This is consistent with the fact that overall the total number of ants in the model swarm most closely matched the number of ants observed in swarm 2. The shape of the density profile of the swarm front (Fig. 20) and the depth (from front to back) of the model swarms matches that measured in real swarms (Chapter 2, Fig. 3). The low-density “pioneer” area at the front of the swarm is considerably shorter in baseline model runs than was measured in real swarms.

Swarm front velocity

Average swarm front velocity measured in the model (3.2 cm / sec, SD = 0.1, N = 20, Table 10) is somewhat higher than those measured in our two data clips (2.19 and 2.1 cm / sec).

Position of faster, “longer,” ants

Distribution of ants in the swarm by size, as measured by maximum running velocity is very consistent with the video data. Although entry of different velocity ants into the arena is randomized, the ants quickly become stratified by peak velocity in a pattern similar to that found in the video clips (Fig. 21).

Effects of parameter variations (Table 10; Fig. 22 - 37)

Swarm front velocity (Fig. 22)

Swarm front velocity varied the most in response to the parameter variations. However, none of the tested parameter variations increased swarm front velocity significantly above baseline. Turning density effects off and reducing strength of ant alignment in response to density interactions reduced swarm front velocity by about one third. Reduced ant release rate also caused a significant reduction in swarm front velocity.
Fig. 20 Representative model outputs under baseline parameters (Table 9). a Map of swarm at 60, 180 and 240 seconds. b Profile of swarm density (ants / 10 cm$^2$) and circular dispersion of ant body angles within the swarm.
Fig. 20 Continued
Fig. 20 Continued
Fig. 21 Spatial distribution of ants in swarm front by “length” as measured by the ant’s maximum possible velocity (see results) at 60 seconds (a) and 240 seconds (b) and in a real swarm (c). Swarm movement is from left to right, with the leading edge of the swarm front on the right.
b $T = 240$ seconds.

c Ant lengths in a temporal cross-section of an *E. burchellii* swarm (see Chapter 2).
Fig. 21 Continued
Table 10 Field measured values, baseline model outputs and results of sensitivity analysis on model outputs.

<table>
<thead>
<tr>
<th>Swarm video results</th>
<th>SF vel in cm / sec (SD)</th>
<th>Mean slope of MCD (SD)</th>
<th>Mean SF density in ants / 10 cm² (SD)</th>
<th>Mean swarm depth in cm (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clip 1</td>
<td>2.19</td>
<td>-0.048</td>
<td>3.08</td>
<td>304.8</td>
</tr>
<tr>
<td>Clip 2</td>
<td>2.10</td>
<td>-0.09</td>
<td>2.17</td>
<td>202.2</td>
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</table>

<table>
<thead>
<tr>
<th>Model results</th>
<th>Variation number</th>
<th>Symbol</th>
<th>Baseline</th>
<th>Value tested</th>
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</thead>
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<tr>
<td>Baseline values</td>
<td></td>
<td></td>
<td></td>
<td>3.223 (0.093)</td>
</tr>
<tr>
<td><strong>Basic Effects</strong></td>
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<td></td>
</tr>
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<td>Pher. Response off</td>
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<td>On Off</td>
<td>3.140 (0.059)</td>
</tr>
<tr>
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<td>–</td>
<td>On Off</td>
<td>1.069 (0.201)</td>
</tr>
<tr>
<td>Low ant release rate</td>
<td>3</td>
<td>–</td>
<td>30 15</td>
<td>1.752 (0.343)</td>
</tr>
<tr>
<td>High ant release rate</td>
<td>4</td>
<td>–</td>
<td>30 50</td>
<td>3.446 (0.072)</td>
</tr>
<tr>
<td>No turn error</td>
<td>5</td>
<td>ε</td>
<td>0.057</td>
<td>0</td>
</tr>
<tr>
<td>High turn error</td>
<td>6</td>
<td>ε</td>
<td>0.057</td>
<td>0.116</td>
</tr>
<tr>
<td><strong>Density Parameters</strong></td>
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</tr>
<tr>
<td>Strong contact alignment</td>
<td>7</td>
<td>τ</td>
<td>5 1</td>
<td>3.341 (0.143)</td>
</tr>
<tr>
<td>Weak contact alignment</td>
<td>8</td>
<td>τ</td>
<td>8 20</td>
<td>1.344 (0.374)</td>
</tr>
<tr>
<td>Rapid Acceleration</td>
<td>9</td>
<td>α</td>
<td>0.9 0.5</td>
<td>3.211 (0.087)</td>
</tr>
</tbody>
</table>
Slow Acceleration 10 a 0.9 0.98 2.654 (0.351) -0.047 (0.024) 3.75 (0.64) 248.39 (52.42)

Pheromone parameters

| Weak pher. response | 11 | γ | 0.05 | 0.025 | 3.101 (0.052) | -0.125 (0.019) | 4.27 (0.11) | 403.86 (18.81) |
| Strong pher. response | 12 | γ | 0.05 | 0.1 | NS | NS | NS | NS |

* SF velocity in video data is mean ΔY of ant movement for all ant paths tracked in areas of density > 1 ant / 10 cm² (Clip 1, 82 paths; Clip 2, 30 paths).

** NS = No swarm front formed, all ants on trails.

Fig. 22 Comparison of model runs to baseline model parameters for mean swarm velocity.
Fig. 23 Comparison of model runs to baseline model parameters for circular dispersion.
Fig. 24 Comparison of model runs to baseline model parameters for swarm density.

Fig. 25 Comparison of model runs to baseline model parameters for swarm depth.
Density-dependent coherence and slope of mean circular dispersion (Table 10, Fig. 23)

Values reported for MCD are the means of the slope of the fitted line for swarm front MCD over the four times sampled. The slope of the MCD is most strongly affected by turning off or reducing pheromone response. Lowering release rate, weakening contact alignment, slowing acceleration and in creasing pheromone response cause a smaller but significant reduction in MCD.

Mean swarm density (Fig. 24)

Increasing ant release rate and acceleration has no significant effect on mean swarm density. Turning density effects off or weakening them significantly reduced swarm front density. Reducing density effects had a lesser but still significant effect on mean swarm front density. Increasing turn error greatly increased swarm density.

Mean swarm depth (Fig. 25)

Swarm depth was the least sensitive to  parameter variations. None of the variations tested reduced swarm depth significantly. Increasing release rate and turn error and slowing acceleration had no significant effect on mean swarm depth. All other parameter variations increased mean depth of the swarm front significantly

Discussion

Our previous work suggests that the complex self-organized foraging swarms of the New World army ant Eciton burchellii are organized through simple rules based on ant reaction to pheromone concentrations and local ant densities and size-based behavioral differentiation (Chapter 2). Using data primarily measured directly from video of army ant swarms taken in the field, we have created a model that closely matches many observed behaviors of army ant swarms. That the baseline model outputs so closely reproduce measured swarming patterns is a strong confirmation of the utility of a data driven approach to studying self-organized processes in complex living systems.

By exploring a selection of key parameters relating to how swarms are organized we have created a strong groundwork for further empirical and modeling work exploring self-organized processes in E. burchellii swarms.

Basic outputs (Table 10)

Swarm front velocity (Fig. 22)

Baseline swarm front velocity in the model (3.2 cm / sec, SD = 0.1, N = 20) was slightly higher than the average swarm velocity measured in the video data (2.15 cm / sec). Swarm front velocities reported in the literature are an order of magnitude slower than this (Chapter 2, Table 1), but reported velocities are averages from a partial or full day’s foraging effort. Swarms typically move forward very swiftly
early in the morning, covering ground at as much as twice these rates (T. Brown, unpublished data). Swarms also move in stops and start, “sprinting” over clear areas and then slowing greatly as the ants encounter substrate variations or areas of high prey abundance (Swartz 1997). It is unknown what a baseline velocity for a swarm would be in an open arena with no prey or variation in substrate. We expect that inclusion of substrate effects and prey in the model would have a significant impact on swarm velocity.

Position of faster, “longer,” ants (Fig. 21)

The only consistent behavioral parameter determined by length found in the video clips was ant velocity. All ants in the model were given the same length and different maximum possible velocities matching the range of velocities found in the data over the range of ant lengths measured. Individual ant velocities at any given model time step are determined by the ant’s maximum possible velocity ($v_{\text{max}}$), adjusted by any slowing caused by density interactions. The distribution of faster, “longer,” ants in the swarm can be measured by plotting the horizontal position and $v_{\text{max}}$ of all ants in the swarm. Although entry of different velocity ants is randomized, the ants quickly become stratified by peak velocity in a pattern similar to that found in the video clips (Fig. 21).

Swarm density (Fig. 25)

In the video clips, the pioneer area of very low ant density (< 0.5 ants / 10 cm²) is as wide as or wider than the width of the main swarm. In the baseline model runs, this area was much shorter than this (1 meter or less). In addition, swarm density was 40 to 60% higher in the model than in the video data. We feel that these two factors are related and that the increased density is a reflection of the shorter pioneer area increasing the number of ants in the main swarm. Reducing release rate or reducing the strength of density effects brings the model swarm front densities more closely in line with the video data. However, it should be noted that the video data is only a temporal snapshot of one small area of two swarms. Swarms in the field show huge spatial and temporal variations in density relating to both substrate effects, prey abundance, colony size and reproductive status (Schneirla 1940 and Chapter 2).

Density-dependent coherence (Fig. 23)

Density-dependent coherence of ant body angles, as measured by slope of MCD, showed considerable variation within the baseline model runs. In early frames (< T – 180), circular dispersion more closely matched that of the video clips. In later frames the slope often changed signs in some frames but not in others. Overall, the outcome of this was that the slope of MCD was significantly lower in the model than in the swarm analyzed. This parameter is a measure of the relationship between ant density and cohesion of motion of ants in the swarm. In the video data, as density exceeded 2.5 ants / 10 cm², ant body angles were seen to become significantly more cohesive as measured by a decrease in MCD slope (Chapter 2, Fig. 4). Of all the swarm parameters tracked, MCD slope was least consistent within model. The low correlation of MCD
slope with density in the model indicates that the density interaction algorithms could be improved. This is not surprising given that the affects of density on turning were not measured directly but were compared for the global frame density of every 50th video frame (Chapter 2). To more accurately understand the relation between density and turning behavior in *E. burchellii*, it would be necessary to directly measure ant density at every frame and match ant turning behavior to local ant density.

Parameter variations (Table 10, Fig. 26 - 37)

Ant release rate (Fig. 28, Fig. 29)

Changing the rate at which ants are released ($R$) has a strong impact on the shape of the swarm front and its forward velocity. A reduction in release rate results in almost no swarm front formation and reduced swarm velocity. Increasing release rate has the opposite impact – the swarm moves forward at a higher velocity and the front portion of the swarm front is much steeper. We believe this change in velocity is a measure of the “outward pressure” created by outgoing described in Chapter 2. As increased numbers of ants attempt to move forward in high density areas, they increase the rate at which the swarm moves forward. The steepness of the swarm front is also increased as more outgoing ants bump into returning pioneers.

Error term (Fig. 30, Fig. 31)

When the turn error term ($\epsilon$) is decreased or turned off, little or no swarm forms and all ants run on trails. When the error term is increased, swarm front velocity is significantly reduced and swarm density is significantly increased. Swarm depth remains similar to the baseline value but the swarm does not move forward. Increasing the turn error term ($\epsilon$), increases swarm width and reduces swarm density because error turn
Fig. 26 Pheromone response off
Fig. 26 Continued
Fig. 27 Density response off.
Time = 60 sec.

Time = 240 sec.

Fig. 27 Continued
Fig. 28 Low ant release rate
Time = 60 sec.

Time = 240 sec.

Fig. 28 Continued
Fig. 29 High ant release rate.
Fig. 29 Continued

Time = 60 sec.

Time = 240 sec.
Fig. 30 No turn error. All ants to stay on trails.
Fig. 30 Continued
Fig. 31 High turn error. Trail system is reduced.
Fig. 31 Continued
Fig. 32 Increased density effects (strong contact alignment).
Fig. 32 Continued
Fig. 33 Reduced density effects (weak contact alignment).
Time = 60 sec.

Time = 210 sec.

Fig. 33 Continued
Fig. 34 Rapid acceleration.
Fig. 34 Continued
Fig. 35  Weak acceleration.
Fig. 35 Continued
Fig. 36 Weak pheromone response.
Fig. 36 Continued
Fig. 37  Strong pheromone response.
Time = 60 sec.

Time = 240 sec.

Fig. 37 Continued
outweighs the ant’s turning response to pheromone. A strong trail system never forms and the swarm’s forward advance is slowed.

Density effects

Contact alignment (Fig. 32, Fig. 33)

When density effects are turned off or substantially reduced through a reduction in the rate at which ants match their body angles, swarm velocity is significantly reduced. We interpret this result to be another affirmation of Schneirla’s hypothesis that “outward pressure” created by outgoing ants plays a significant role in moving the swarm forward. As density effects are reduced, the swarm has difficulty in determining a consensus travel direction and does not move forward as quickly. An additional effect of reduced density interactions is that outgoing ants are not slowed by returning pioneer ants. This produces a less dense and wider swarm front with a less abrupt leading edge.

Increasing density response ($\tau$), such that ants align themselves more quickly with encountered ants, increased swarm velocity slightly but this effect was not significant (Table 10, Fig. 22). Analysis of this parameter indicates that increasing the strength of the ants’ reaction to their neighbors forces the ants in the dense part of the swarm to move with greater unity by reducing their ability to turn against the mean direction of the swarm. It is likely that the observed velocity increase with faster response to density results from a concurrent reduction in overall turning rate as well as a reduction in the slowing effects of interactions between pioneers.

Acceleration constant (Fig. 34, Fig. 35)

Changing the acceleration constant ($\alpha$) affects density interactions similarly to changing the strength of the alignment response to density parameter ($\tau$). When the acceleration constant is set to the baseline value (0.9), ants typically take about $\frac{1}{2}$ second to regain their initial maximum velocity. When the acceleration constant is low (rapid acceleration), ants only slow for one or two steps when encountering other ants. This reduces the number of steps during which one ant can perceive another, and so ants only briefly interact. A reduction in length of interaction time reduces the strength of interaction between outgoing ants and returning pioneers. The outcome is reduced swarm density (Fig. 24) and a wider swarm front (Fig. 25). Increasing the length of time an ant is slowed by an interaction has the opposite effect, swarm depth and width decrease.

Pheromone variations (Fig. 36, Fig. 37)

Turning off pheromone response completely causes an increase in swarm velocity and results in a total lack of trails. When pheromone response is turned off and ants have no random component ($\epsilon$) to their turns, they move forward in a grid pattern and swarm velocity is higher than normal (not shown). When pheromone response is off, but a random turn component is included, swarm front velocity also increases but to a lesser extent because ants exhibit a more diverse range of angles and are more likely to be slowed by interactions.
Increasing the strength of pheromone response ($\gamma$) slows the swarm because ants turn so strongly towards pheromone that forward motion is reduced. Increased $\gamma$ acts on swarm depth similarly to reduce density response (i.e., slow acceleration and weak alignment) because the ants turn so strongly to pheromone that their turning in response to density is overwhelmed. With lowered pheromone response the swarm becomes wider and less dense because pioneer ants are less likely to turn back after encountering areas of low pheromone.

Conclusions

The combination of detailed empirical and modeling work described in this chapter is a very effective way to examine self-organized processes. In the process of describing and modeling the swarming rules used by *E. burchellii*, we have developed a set of tools permitting measurements of key descriptive parameters relating to swarm organization which can be equally applied to both real swarms and the model. Developing such measures is essential for furthering both our understanding of how *E. burchellii* army ant swarms are organized and for improving the swarm model. This work suggests a number of improvements that would further our knowledge of the system. First, to truly understand how *E. burchellii* army ants response to density and pheromone, it is necessary to know the position of all ants at all times in swarm videos. This will be possible only when better tracking software has been developed that permits automated tracking of ants in field recorded video. Secondly, our knowledge of pheromone deposition behavior in army ants is woefully inadequate. Further research is needed to clarify if pheromone deposition is continuous and whether or not different size of ants or ants at different places in the swarm may lay trail pheromone differently. This question can also be addressed through further modeling work and through numerical exploration of the larger datasets that will be provided by improved tracking software. Finally, the model should be extended to include the effects of substrate and prey appearance. As computer processing power increases, it will be possible to run the model with greater swarm sizes and over larger spatial areas with more realistic management of density and pheromone.
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