
Short Communication

The Blind Leading the Blind: Modeling Chemically Mediated Army Ant Raid Patterns

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INTRODUCTION

Army ant colonies are among the largest and most cohesive societies. Individual ants are typically less than 10 mm long, communication between them is restricted to local chemical and tactile stimuli, and yet their foraging systems coordinate hundreds of thousands of individuals and cover some 1000 m² in a day (Fig. 1) (Raignier and Van Boven, 1955; Rettenmeyer, 1963; Schneirla, 1971; Topoff, 1972; Gotwald, 1982; Franks and Fletcher, 1983; Burton and Franks, 1985). Such swarm raids pose in the strongest possible way the general problem of collective decision making without any form of centralized control. Our model shows how their characteristic patterns could be self-organizing, i.e., generated from the interactions between many identical foragers, each with simple trail-laying and trail-following behavior.

MODEL AND MONTE CARLO SIMULATIONS

Unlike most other ant species, army ant foragers lay pheromone not only when returning with prey but also, to a lesser extent, while advancing with the swarm (Schneirla, 1933, 1940). If we consider the swarm to move in a discrete network of points representing continuous two-dimensional (2-D) space (Fig. 2, inset), at each point each ant chooses ahead left or ahead right, moves, and adds to the pheromone at the point chosen. Initially, the choice is random.

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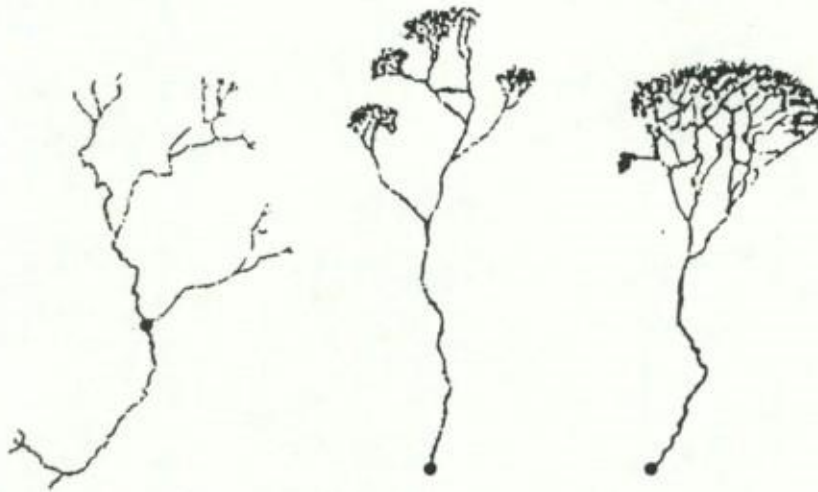


Fig. 1. Foraging patterns of three army ants, *Eciton hamatum*, *E. rapax*, and *E. burchelli* (from left to right), each covering some 50 × 20 m. [Redrawn from Rettenmeyer (1963) and Burton and Franks (1985).]

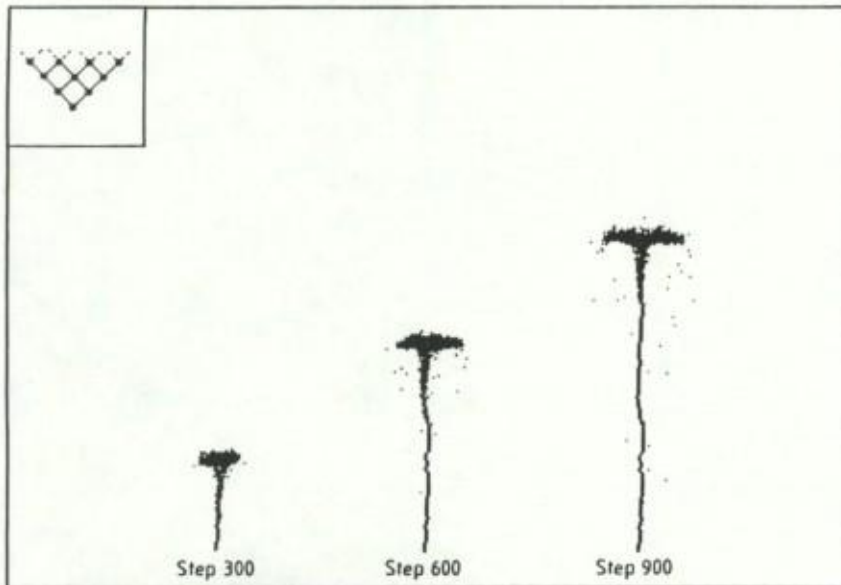


Fig. 2. Monte Carlo simulation of the model on a network of points representing 2-D space (inset). At each point, prob. (choosing left) = 1 - prob. (choosing right) = $[\frac{1}{5} + P_r] / [(5 + P_l)^2 + (5 + P_r)^2]$, where P_l and P_r are the quantities of pheromone ahead left and right. Prob. (moving per step) = $\frac{1}{2} + \frac{1}{2} \tanh [(P_l + P_r) / P_{1/2} - 1]$. $e = \frac{1}{50}$, $P_{1/2} = 100$, P_{sat} (advancing ants) = 1000, and P_{sat} (returning ants) = 300. Ten ants leave the nest per step. Maximum number of ants per point = 20. The unit for P is the quantity of pheromone laid by an advancing ant per point. Returning ants lay 10 pheromone units per point.

However, in marking, each ant that passes a point modifies the following ant's probability of choosing left or right, an autocatalytic system that rapidly leads to a symmetry breaking, one of the two points ahead becoming more or less completely preferred to the other. This process, repeated at each point along the swarm's path, is the basis of how the swarm forms its trails.

This model is subject to three refinements. First, it is observed that the foragers on the trail move rapidly and directly (Schneirla, 1940; Franks, 1985), whereas those at the front are much slower, more hesitant and random, making characteristic looping movements. This is linked to the fact that the trail is extremely well marked, while the leading edge of the front is unmarked. We simulate this by making the probability of each ant's moving at each step increase sigmoidally with the pheromone quantity ahead of it.

Second, there is a maximum number of ants that can occupy one point. At each point the foragers decide whether to move and, if so, whether to move ahead left or ahead right. Should the point ahead right not have enough room for all those wishing to move there, the surplus move ahead left instead, and vice versa. Should both points ahead be full, then the surplus ants stay where they are [cf. Schneirla's (1940) pressure/drainage analogy].

Third, a fixed fraction, e , of the pheromone at each point evaporates per step. Only moving ants lay pheromone, at the point at which they arrive, although not if the quantity of pheromone there is greater than a saturation value, P_{sat} .

Figure 2 shows a Monte Carlo simulation of this model. The choice function proposed is based on an experimental study of similar but smaller exploratory swarms in the Dolychoderine ant, *Iridomyrmex humilis* (Deneubourg *et al.*, 1989), and an analytical model (Deneubourg, 1979). A diffuse front is formed and advances with a concentrated trail extending from its trailing edge to the nest. At the front, the ground is relatively unmarked and the ants move slowly and randomly, thus accumulating and spreading out. At the trailing edge of the front, the number of passages is sufficient for one path, the trail, to have become preferred to all other possibilities.

So far we have defined only ants that advance, but what about those that return? We state that they return when they have found a food item. How is the food distributed? We first consider that each point has a fixed probability of containing one nonrenewable food item, transportable by one ant. This approximates the situation of *Eciton burchelli*, which feeds largely on scattered arthropods (Franks and Bossert, 1983).

The first ant that arrives at a point containing a food item takes it and returns toward the nest, obeying exactly the same rules as an advancing ant, laying, however, a greater amount of pheromone per step. Arriving at the nest, it lays down the food item and return outward once more. (Note that should there be at any point no guiding pheromone in front of them, they move toward the central trail although this rule is only rarely invoked.)

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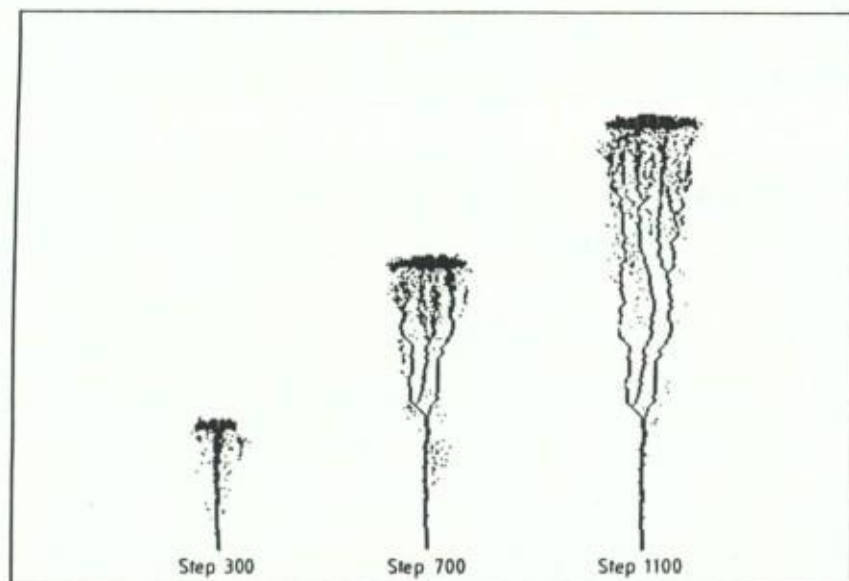


Fig. 3. The same as Fig. 2, with each point having a 1-in-2 probability of containing one food item.

With a low food density, the returning ants do not modify the swarm pattern seen in Fig. 2. However, with higher densities, they cause the central trail to split into lateral trails which themselves branch out, giving a swarm like a river delta (Fig. 3), characteristic of *E. burchelli*. As the swarm advances the older lateral trails are progressively abandoned, while new ones are formed just behind the diffuse front.

Finally, *E. hamatum* feeds more on dispersed social insect colonies, and its food distribution can be represented by each point having a very small probability of containing a very large number of food items. *E. rapax* has an intermediary diet. With this more heterogeneous food distribution, the swarm splits up into a number of small columns and deltas (Fig. 4), characteristic of *E. rapax* [see also Moffet (1988) for the different patterns of *Pheidologeton diversus* when presented with dispersed or concentrated food sources].

DISCUSSION

It is known that the army ant syndrome has evolved convergently at least seven times (Wilson, 1958) and that "group raiding" behavior is found in a number of distantly related social insects (Pasteels, 1965; Stuart, 1969; Maschwitz and Mühlenberg, 1975; Leuthold *et al.*, 1976; Oloo and Leuthold,

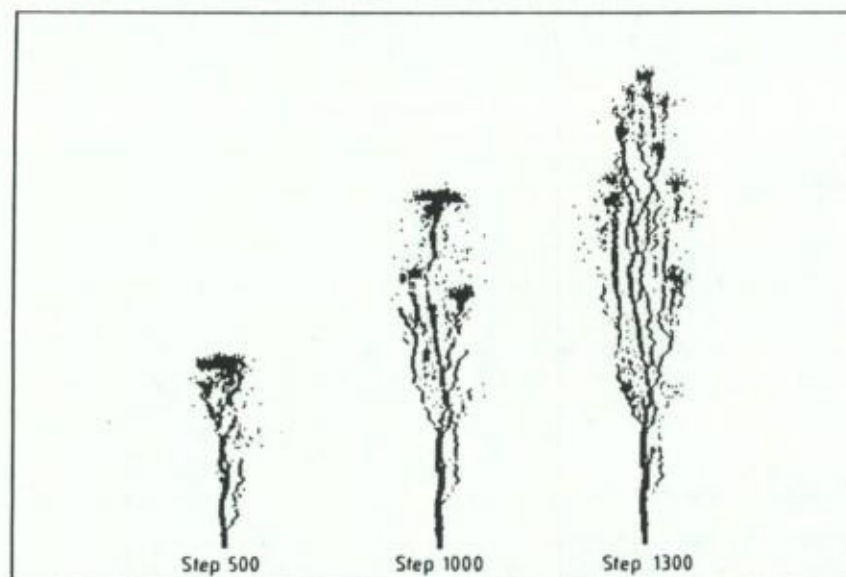


Fig. 4. The same as Fig. 3, with each point having a 1-in-100 probability of containing 400 food items.

1979; Hölldobler *et al.*, 1982; Moffet, 1984) and even in some gregarious caterpillars (Fitzgerald and Peterson, 1988). This appears less surprising if we consider the essential simplicity of the mechanism needed to coordinate the very large numbers of participants, namely, laying trail-pheromone both while advancing and while returning. Furthermore, the manner in which the environment determines the different swarm patterns leads us to suggest that they originally arose from the same behavior associated with different prey preferences and that gradually additional mechanisms evolved to reinforce and accentuate these patterns, which then became species specific.

For example, Chadab and Rettenmeyer (1975) showed how a single *E. hamatum* forager can divert nestmates from a dense foraging column toward an important food source, using tactile stimuli and probably a different chemical signal from that used on the main foraging trails, thereby accentuating the swarm's branching. Topoff *et al.* (1980) have shown a similar behavior in *Neivamyrmex nigrescens*. (Note that while the model does not distinguish between exploration and recruitment, considering the same pheromone to be used in both processes, those that return with food lay considerably more trail pheromone than those advancing and are responsible for the branching observed in Figs. 3 and 4.) Schneirla's (1940) pressure/drainage analogy also accentuates the role

of physical contact between workers. Nevertheless, in our wish to stress how maximum collective complexity can be compatible with maximum individual simplicity, we have ignored these and other possible factors, such as surface heterogeneity, that may influence the swarm's pattern.

We have shown how swarm patterns can result from the interplay between chemical communication and food exploitation. While most ant and termite species do not exhibit legionary behavior (and do not lay trail pheromone as they explore), the majority nevertheless relies on trail pheromone to coordinate their foraging activity. The basic script is simple. A number of scouts leave the nest. Those that find food return, laying a trail whose strength depends on the size and quality of the food, the forager's species, etc. Other foragers waiting in the nest follow these trails more or less successfully. Taking into account specific characteristics such as colony size, type, and distribution of prey, etc., a small set of simple rules similar to those presented for the army ants could explain many different types of spatiotemporal forager distribution (Goss and Deneubourg, 1989, in preparation), such as the formation of trunk-trails (Hölldobler and Lumsden, 1980), the selection of the best food sources (Pasteels *et al.*, 1987), the sequential exploitation of contiguous foraging zones (Bernstein, 1975; Franks and Fletcher, 1983), and the switch from diffuse to concentrated foraging (Hahn and Maschwitz, 1985).

All these systems have in common simplicity and equality of the individuals, communicating chemically with a single pheromone. These minimalistic assumptions, deliberately ignoring other factors such as age and memory, are justified in that we wish to show the role and limits of such self-organization mechanisms. The resulting structures are dynamic and adapt as the actors interact with the environment, conferring a degree of intelligence to the society that far exceeds the capacity of its individual members.

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REFERENCES

- Bernstein, R. A. (1975). Foraging strategies of ants in response to variable food density (Hym. Formicidae). *Ecology* **56**: 213-219.
- Burton, J. L., and Franks, N. R. (1985). The foraging ecology of the army ant *Eciton rapax*: An ergonomic enigma? *Ecol. Entomol.* **10**: 131-141.
- Chadab, R., and Rettenmeyer, C. W. (1975). Mass recruitment by army ants. *Science* **188**: 1124-1125.
- Deneubourg, J. L. (1979). *Essai de Modélisation en Sociobiologie et Sociologie*. Ph.D. thesis, Université Libre de Bruxelles, Bruxelles.

- Deneubourg, J. L., Aron, S., Goss, S., and Pasteels, J. M. (1989). The self-organizing exploratory pattern of the Argentine ant. *J. Insect Behav.* (in press).
- Fitzgerald, T. D., and Peterson, S. C. (1988). Cooperative foraging and communication in caterpillars. *Bioscience* **38**: 20-25.
- Franks, N. R. (1985). Reproduction, foraging efficiency and worker polymorphism in army ants. In Hölldobler, B., and Lindauer, M. (eds.), *Experimental Behavioral Ecology: Fortschritte der Zool. BD 31*, Fischer Verlag, Stuttgart, pp. 91-107.
- Franks, N. R., and Bossert, W. H. (1983). The Influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. In Sutton, S. L., Chadwick, A. C., and Whitmore, T. C. (eds.), *Tropical Rain Forest: Ecology and Management*, Blackwell, Oxford, pp. 151-163.
- Franks, N. R., and Fletcher, C. R. (1983). Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behav. Ecol. Sociobiol.* **12**: 261-270.
- Goss, S., and Deneubourg, J. L. (1989). The self-organising clock-pattern of *Messor pergandei* (Formicidae, Myrmicinae). *Insect Soc.* (in press).
- Gotwald, W. H., Jr. (1982). Army ants. In Hermann, H. R. (ed.), *Social Insects*, Academic Press, New York, pp. 157-254.
- Hahn, M., and Maschwitz, U. (1985). Foraging strategies and recruitment behaviour in the European harvester ant *Messor ruftarsis* (F.). *Oecologia* **68**: 45-51.
- Hölldobler, B., and Lumsden, C. J. (1980). Territorial strategies in ants. *Science* **210**: 732-739.
- Hölldobler, B., Engel, H., and Taylor, R. E. (1982). A new sternal gland in ants and its function in chemical communication. *Naturwissenschaften* **69**: 90-91.
- Leuthold, R. H., Bruinsma, O., and van Huis, A. (1976). Optical and pheromonal orientation and memory for homing distance in the harvester termite *Hodotermes mossambicus* (Hagen) (Isopt., Homotermitidae). *Behav. Ecol. Sociobiol.* **1**: 127-139.
- Maschwitz, U., and Mühlberg, M. (1975). Zur jagdstrategie einiger orientalischer Leptogenys-Arten (Formicidae: Ponerinae). *Oecologia* **38**: 65-83.
- Moffet, M. W. (1984). Swarm raiding in a myrmicine ant. *Naturwissenschaften* **71**: 588-590.
- Moffet, M. W. (1988). Foraging dynamics in the group-hunting myrmicine ant, *Pheidologeton diversus*. *J. Insect Behav.* **71**: 588-590.
- Oloo, G. W., and Leuthold, R. H. (1979). The influence of food on the trail-laying and recruitment behaviour in *Trinervitermes bettonianus* (Termitidae: Nasutitermitinae). *Entomol. Exp. Appl.* **26**: 267-278.
- Pasteels, J. M. (1965). Polyéthisme chez les ouvrières de *Nasutitermes lujae* (Termitidae Isoptères). *Biol. Gabon.* **1**: 191-205.
- Pasteels, J. M., Deneubourg, J. L., and Goss, S. (1987). Self-organization mechanisms in ant societies (I): Trail recruitment to newly discovered food sources. In Pasteels, J. M., and Deneubourg, J. L. (eds.), *From Individual To Collective Behavior In Social Insects*, Birkhäuser, Basel, pp. 155-176.
- Raignier, A., and Van Boven, J. K. A. (1955). Etude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera: Formicidae). *J. Ann. Mus. Roy. Congo Belge n.s. 4 Sci. Zool.* **2**: 1-359.
- Rettenmeyer, C. W. (1963). Behavioral studies of army ants. *Univ. Kans. Sci. Bull.* **44**: 281-465.
- Schneirla, T. C. (1933). Studies on army ants in Panama. *J. Comp. Psychol.* **15**: 267-299.
- Schneirla, T. C. (1940). Further studies on the army ant behavior pattern. *J. Comp. Psychol.* **29**: 401-461.
- Schneirla, T. C. (1971). In Topoff, H. R. (ed.), *Army Ants: A Study in Social Organization*, Freeman, San Francisco.
- Stuart, A. M. (1969). Social behavior and communication. In Krishna, K., and Weesner, F. M. (eds.), *Biology of Termites*, Academic Press, New York, pp. 193-232.
- Topoff, H. R. (1972). The social behavior of army ants. In Eisner, T., and Wilson, E. O. (eds.), *The Insects*, Scientific American, Freeman, San Francisco, pp. 247-262.
- Topoff, H. R., Miranda, J., Droual, R., and Herrick, S. (1980). Behavioural ecology of mass recruitment in the army ant *Neivamyrmex nigrescens*. *Anim. Behav.* **28**: 779-789.
- Wilson, E. O. (1958). The beginnings of nomadic and group-predatory behavior in the ponerine ants. *Evolution* **12**: 24-31.

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