The Self-Organizing Exploratory Pattern of the Argentine Ant

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Workers of the Argentine ant, Iridomyrmex humilis, *start to explore a chemically unmarked territory randomly. As the exploratory front advances, other explorers are recruited and a trail extends from it to the nest. Whereas recruitment trails are generally constructed between two points, these exploratory trails have no fixed destination, and strongly resemble the foraging patterns of army ants. A minimal model shows how the exploratory pattern may be generated by the individual workers' simple trail-laying and -following behavior, illustrating how complex collective structures in insect colonies may be based on self-organization.*

INTRODUCTION

A social insect colony is a superorganism . . . without a brain, and each worker has access to only very local information. How then is a colony capable of complex, collective behavior? One approach to this question considers a colony as a collection of genetically preprogrammed specialists (Oster and Wilson, 1978), whose number and activity are regulated by negative feedback and mass-communication (Wilson and Hölldobler, 1988). However, to understand the spatial exploratory pattern of the Argentine ant *Iridomyrmex humilis* reported here, it is necessary to use an opposite and complementary approach, in which the collective pattern is seen as resulting from autocatalytic interactions between simple, identical explorers. Such emergent collective behavior is designated by

the term self-organization, following an identical use in other natural systems (Nicolis and Prigogine, 1977; Schieve and Allen, 1982; Prigogine and Stengers, 1984).

In this case the autocatalysis (one explorer's movements being determined by those of previous explorers) is mediated by trail pheromone. While most ant species are known to lay trail pheromone only when returning to the nest from an important food source, we have shown that trail pheromone is laid by *I. humilis* explorers more or less continually during an exploratory recruitment, in the absence of any food source, and determines the explorers' movements. A hexanic extract of an exploratory trail induces trail-following and contains Z-9-hexadecenal [first isolated in Pavan's gland by Cavill *et al.* (1979)]. The explorers follow pheromonal cues rather than visual ones (Aron and Pasteels, 1988; Aron *et al.*, 1989). They even form their characteristic exploratory pattern in the dark (Aron, unpublished). Previously, Van Vorhis Key and Baker (1986) have shown that *I. humilis* foragers lay the same pheromone both when leaving and when returning to the nest during a food recruitment.

In this paper we concentrate uniquely on explaining how the collective exploratory pattern is generated from the individual ants' trail-laying and trail-following behavior. First, we describe the exploratory pattern. Second, an experimental device is used to reduce the explorers' movements to a simple binary choice. Together with a mathematical model, this allows a quantification of the way in which an individual explorer's choice is modified by the previous choice of other explorers via the pheromone they have laid. Finally, the model and parameters evaluated by this analysis are used to generate the collective pattern observed in the arena.

MATERIALS AND METHODS

Exploration of the Chemically Unmarked Arena

Laboratory colonies of *I. humilis* (150–1200 workers) were given access to an arena (0.8 × 0.8 m) covered with white sand by placing a bridge between the nest container. Photographs of the arena were taken every minute to monitor the exploring ants' spatial distribution. Food was never present. It suffices to change the sand in a well-explored arena to reinduce collective exploration.

Exploration Traffic on a Diamond-Shaped Bridge Between Nest and Arena

In order to study the passage from the uncoordinated state (the diffuse front) to the coordinated state (the exploratory trail), we introduced a diamond-shaped bridge (Fig. 2 inset) between the nest and the chemically unmarked arena. The

explorers on the bridge are presented with only one binary left/right choice, and the dynamics of their cumulative choice can be easily quantified.

The angle between the branches was acute (60°), so that on leaving a branch the vast majority of ants continued directly toward the arena if leaving the nest, or toward the nest if returning, and very few doubled round from one branch on to the other. The distance between the two forks was 15 cm. The traffic on each branch of this bridge was counted in 3-min intervals.

RESULTS

Exploration of the Chemically Unmarked Arena

When a laboratory colony of *I. humilis* is given access to a chemically unmarked arena, its workers explore randomly the part closest to the nest. As the exploratory front advances into the arena, a trail extends from it to the nest (Fig. 1), and the number of explorers grows logistically, indicating recruitment. If the returning explorers are removed before they can return to the nest, the exploration is prevented from developing. Collective exploration was never observed on a well-explored arena unless the sand was replaced.
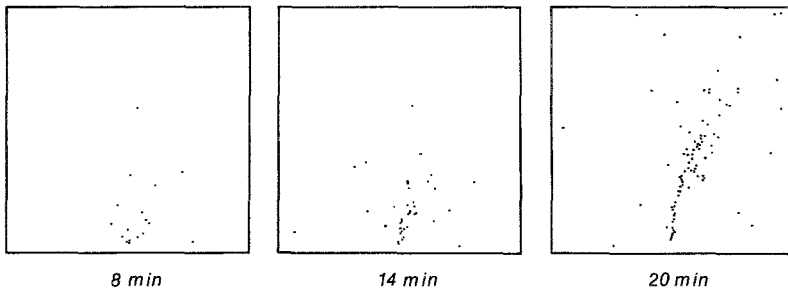

8 min   14 min   20 min

Fig. 1. Exploratory pattern on an 0.8 × 0.8-m sandy arena. Colony of 600 workers. Each point represents one ant.

Exploration Traffic on a Diamond-Shaped Bridge Between Nest and Arena

Initially both branches are chosen equally. However, in marking, each ant that passes modifies the following ant's probability of choosing left or right, a positive-feedback system that, after initial fluctuation, rapidly leads to one of the two forks becoming more or less completely preferred to the other. This symmetry breaking, repeated at each point the explorers pass, is the basis of how the trail is formed (see below).

In this article we estimate the pheromone quantity at a point by the number

of ants that have passed the point. This involves two simplifications that do not influence the pattern generated. First, we ignore the pheromone's evaporation, as its mean lifetime may be estimated (from the data of Van Vorhis Key and Baker, 1982) to be of the order of half an hour, while plateau values are reached after 10–25 min in our experiments. Second, we consider that each ant lays an average amount of pheromone, whether leaving or returning to the nest, although there is a certain degree of individual variability in trail-laying and ants are slightly more active in laying pheromone when returning (Aron *et al.*, 1989). The kinetics of the ants' choice can therefore be represented not only as a function of time but also as a function of the cumulative number of ants passing the point.

Figure 2 shows the results of one exploration as a function of time, and Fig. 3 pools the results from 20 different experiments on different colonies, with somewhat variable recruitment dynamics, as a function of the number of ant passages. The dashed curve in Fig. 3 represents the average and clearly shows how the probability of an explorer choosing what is ultimately the collectively selected branch increases rapidly and nonlinearly with the number of explorers that have previously passed on the bridge.

Monte Carlo Simulations of Exploration on the Diamond-Shaped Bridge

The exploration on the bridge is modeled as follows. After i ants have crossed the bridge there are i pheromone units on the bridge, of which A_i are on branch A, and B_i on branch B. The next ant arriving chooses branch A or B
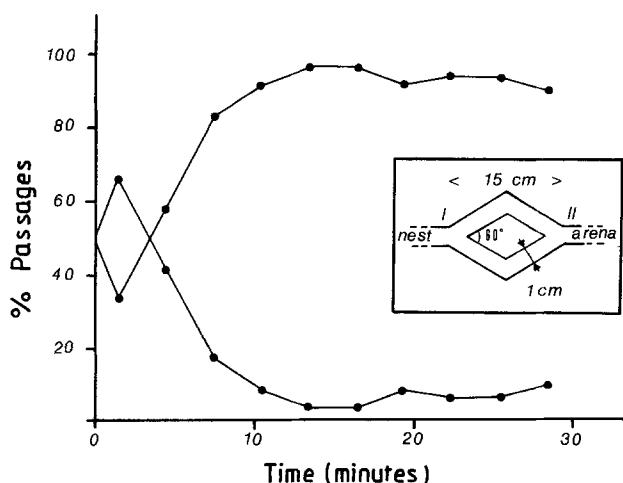

Fig. 2. Percentage of ants per 3-min period passing on the two branches of the bridge (inset). Colony of 1000 workers.
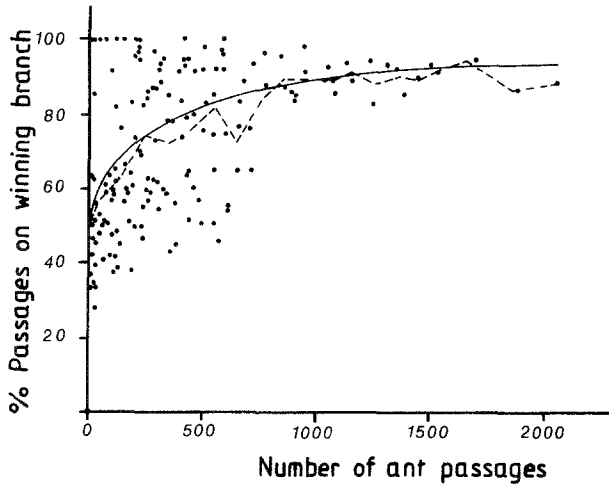
Fig. 3. Percentage of ants passing on the collectively selected branch of the diamond-shaped bridge: 20 experiments, nine colonies of 150–1200 workers, measured every 3 min for 30 min (points). The horizontal axis represents the cumulative number of ant passages on the bridge (i.e., on both branches). The dashed curve represents the average values calculated every 100 ant passages. The solid curve represents the average of 200 Monte Carlo simulations, based on Eqs. (1) and (2), with $n = 2$ and $k = 20$.

with probabilities $prob_A$ and $prob_B$, depending on A_i and B_i (i.e., on the number of ants that have previously chosen each branch). Having chosen, the ant then adds to the pheromone on the branch chosen. Thus:

$$prob_A = \frac{(k + A_i)^n}{(k + A_i)^n + (k + B_i)^n} \qquad (prob_A + prob_B = 1) \quad (1)$$

$$A_{i+1} = A_i + \delta, \qquad B_{i+1} = B_i + (1 - \delta) \qquad (A_i + B_i = i) \quad (2)$$

where δ is a stochastic variable that takes a value of 1 or 0 with probability $prob_A$ and $prob_B$, respectively. In other words, A is increased by one unit if the ant chooses branch A; otherwise it chooses branch B and adds to B.

Equation (1) is a simple general choice function, which quantifies the way in which a higher concentration on branch A gives a higher probability of choosing branch A, depending on the absolute and relative values of A_i and B_i. The parameter n determines the degree of nonlinearity of the choice, a high value of n meaning that if one branch has only very slightly more pheromone than the other, the next ant that passes will have a very high probability of choosing it. The parameter k corresponds to the degree of attraction attributed to an

unmarked branch, or in other words, the greater k, the greater the marking necessary for the choice to become significantly nonrandom.

The Monte Carlo simulations of the model work by comparing, for each successive ant, a random number generated by computer with the probability of choosing branch A or B as determined by Eq. (1). Figure 3 shows that Eq. (1) can provide an accurate description of the *I. humilis* explorers' choice. By matching the experimentally observed ants' choice of branch on the bridge with Monte Carlo simulations (dashed vs solid curves), the values of n and k have been fitted empirically, giving $n \approx 2$ and $k \approx 20$. Thus, the first ant that crosses the bridge will, of course, choose branch A with a probability of 0.5, i.e., $20^2/(20^2 + 20^2)$. If it chose branch A, the second ant will choose branch A with a probability of 0.524, i.e., $21^2/(21^2 + 20^2)$, and so on.

Monte Carlo Simulation of Exploration on the Chemically Unmarked Arena

Now that the way in which the choices of successive explorers lead to the collective selection of one of two possibilities has been quantitatively analyzed, we can piece together a succession of such selections to represent how the explorers move in two-dimensional (2-D) space and progressively form the exploratory trail behind the exploratory front.

We reduce continuous 2-D space to a simple network of discrete points in which each point leads to two others (Fig. 4 inset), this being the equivalent of a very large number of interconnecting bridges. At each point an ant can move to only one of the two points ahead of it, choosing and marking according to Eqs. (1) and (2). We have also limited an explorer's orientation within this network to two overall directions, namely, away from the nest and returning to the nest, corresponding to their observed general directional inertia.
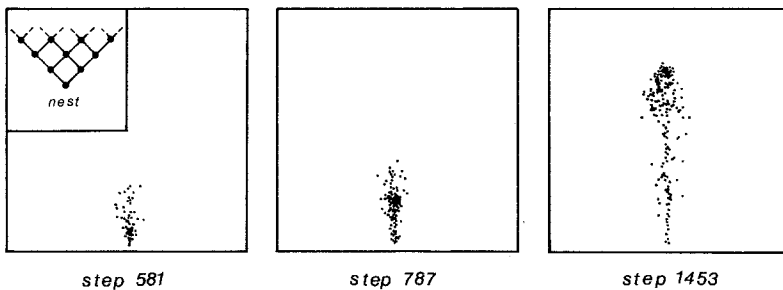

step 581   step 787   step 1453

Fig. 4. Monte Carlo simulation of exploration of a 2-D network (inset), based on Eqs. (1) and (2), with $n = 2$ and $k = 20$. Each ant at each point and step has a probability of moving $= \frac{1}{2} + \frac{1}{2} \tanh [(A_i + B_i)/100]$. Each point represents at least one ant. Number of ants (N) $= 300$. Number leaving nest per step $= (0.0001 + 0.00002 X) (N - X)$, where $X = $ No. outside nest. Probability of returning $= 0.0034$ per ant per step.

Two further simplifications have been made. First, the rate at which explorers leave or return to the nest is highly variable and does not greatly influence the collective pattern generated. We have used a simplified logistic-type approximation of the observed recruitment dynamics to generate the ants leaving the nest, and each explorer has a fixed probability of deciding to return to the nest per step (see legend to Fig. 4). Second, the explorers do not necessarily move at each step. It is observed experimentally that the ants at the front, where there is as yet little or no marking, move hesitantly and randomly, while those on the well-marked trail move faster and in a straight line. Accordingly, the probability of moving per time step in the simulation is made to increase sigmoidally with the pheromone quantity ahead of the point in question (see legend to Fig. 4).

Figure 4 presents a Monte Carlo simulation of explorers moving on this network. The advance of the diffuse front and the formation of the trail behind it are clearly reproduced. At the front, the territory is unmarked and the ants move slowly and randomly, thus accumulating in number and spreading out. At the trailing edge of the front, the pheromone concentration is higher and a single path, the newest segment of the trail has become preferred to all other possibilities. Only a small percentage of ants leaving the nest strays off the trail before arriving at the front.

Note that the simulation generates the same pattern if only the advancing explorers lay pheromone. If only the returning explorers mark, however, the pattern is a lot less apparent, because of their much smaller number and because they return from widely separated points.

Other more complicated discrete networks with more choices at each point are possible but would, at most, have the effect of generating potentially more sinuous trails, without adding to our understanding of how the exploratory trail is formed. However, both experiments and simulations generate highly linear exploratory trails, justifying the above-mentioned limitations on the explorers' orientation and the simple network in the model.

The ants that have become separated from the main body of explorers appear more dispersed in the experiments than in the simulations (Fig. 1 vs Fig. 4). Different factors contribute to this. First, the model excludes any orientation perpendicular to the arena's central axis, i.e., a choice between ahead left and back left, or a choice between ahead right and back right. Second, returning ants arriving at a point where there are no marks to guide them are forced in the simulations to choose the direction toward the arena's central axis [this unique exception to Eqs. (1) and (2) is rarely invoked]. Third, real-life explorers that have reached a wall move along it rather than back into the arena (the edge effect).

The 2-D simulations nevertheless show how the interactions among the individual explorers, whose trail-laying and trail-following behavior is reduced to its simplest expression, generate all the features of the complex collective pattern observed.

DISCUSSION

I. humilis' exploratory behavior is exceptional in that they mark continually and explore collectively. Whereas other recruitment trails are constructed between two points (e.g., nest and food), their exploratory trails have no known destination, progressively advancing into the unknown. They rapidly lead new explorers to the frontier between the just explored and the about to be explored zones, avoiding exploring the same zone twice, and help returning explorers reach the nest directly. A wide corridor of the chemically unmarked area is thus systematically "swept" and marked in a minimum time with maximum economy, just as a broom with a wide brush (the front) and a narrow handle (the trail) sweeps a corridor. A highly similar exploratory pattern may be seen in the termites *Nasutitermes lujae* (Pasteels, 1965) and *Trinervitermes geminatus* (Rickli and Leuthold, 1986) as well as in the ants *I. pruinosus* and *Solenopsis* sp. (Hölldobler, personal communication).

These "exploratory swarms" are also remarkably similar to army ant-type foraging swarms (Rettenmeyer, 1963; Schneirla, 1940, 1971; Topoff, 1972; Moffet, 1984, 1988; Franks and Fletcher, 1983), albeit on a much smaller scale. The similarity is seen both at the individual and the collective level, and the same basic model may be used for both (Deneubourg *et al.*, 1989). Such collective exploration/foraging could well be a characteristic of species with very large colonies (see also Gordon, 1988), many of which, because of their size, rely to a great extent on pheromonal communication to coordinate their workers' activity outside the nest.

The simplicity of the mechanisms involved, and Occam's principle of scientific parsimony, leads us to speculate that only two conditions are necessary for this phenomenon to appear. The workers outside the nest must continually lay pheromone and must leave the nest together in sufficient numbers. For the latter point, it is perhaps significant that *I. humilis* explorers mark with a pheromone that not only guides but recruits (Van Vorhis Key and Baker, 1982, 1986; Aron *et al.*, 1989). In this light, collective exploration might be seen as an unexpected bonus that not only appears inevitably whenever the two conditions are met, but moreover, need not be explicitly coded into the individual behavior. Indeed if one considers how many different and complicated "instructions" would be necessary explicitly to coordinate a swarm, one may readily appreciate both the genetic economy and the added reliability that come with such simplicity.

Finally, the basic autocatalytic mechanism involved in this chemical trail formation is not restricted to group exploration or group foraging or to chemical trails. An analogy may be made between the formation of trails, for example, by mammals in scrub or grassland or even by students on a snowed-under campus! The more animals that have passed at one point, the more the vegetation

is trampled, the less resistance it offers, and the more likely the following animal is to take that path, and so on.

By the same mechanism, *I. humilis'* chemical trail in the sandy arena was often seen to become a physical trail as well, in the sense that the ants repeated passage led to the formation of a "valley" which surely reinforced their preference. Similar physical trails are seen in a number of other ant species, trunk trails along which the vegetation is visibly prevented from growing.

Such phenomena fall into the class of nonlinear Polya processes, which describe the additive evolution of the number of "individuals" in a finite number of categories, the category of each new individual added being a function of the proportions of each category present (Arthur *et al.*, 1986).

Similar processes may be seen in widely varied "social" phenomena, such as termite nest building (Grassé, 1939, 1959; Deneubourg, 1977), individual and collective ant foraging patterns (Pasteels *et al.*, 1987; Deneubourg *et al.*, 1987; Goss and Deneubourg, 1989), rhythmically synchronized activity in ants (Goss and Deneubourg, 1988), slime-mold aggregation (Keller and Segel, 1970), intertidal mollusk movement (Focardi *et al.*, 1985), and also the generation of physical and chemical spatial instabilities (Turing, 1952; Nicolis and Prigogine, 1977; Haken, 1983).

ACKNOWLEDGMENTS

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