Self-organizing Spatial Patterns in the Argentine Ant
*Iridomyrmex humilis* (Mayr)

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INTRODUCTION

Two conspicuous characteristics of the Argentine ant, *Iridomyrmex humilis*, are its highly agonistic and opportunistic behaviors. Originating in South America, this species spread to most temperate and sub-tropical zones of Australia, South Africa, North America, and Europe. Once installed, *I. humilis* eliminates native ants through continuous warfare and exploits a maximum range of food sources, destroying buds, blooms and fruits of crops such as sugar cane, coffee and lemons (Newell, 1908; Crowell, 1968; Markin, 1970; Fluker and Beardsley, 1970; Erickson, 1971; Bond and Slingsby, 1984; Ward, 1987). In addition, the ants attend and protect numerous scale insects and plant lice from natural predators, leading to large population increases of Coccidae and Aphididae and failure of natural control (De Bach et al. 1951; Samways et al. 1982; Dreistadt et al. 1986; Haney et al. 1987). The Argentine ant is considered a major economic pest.

Their ecological success depends on at least three factors: (1) they tolerate a wide range of habitats as long as there is sufficient moisture in logs, under rocks or in the ground; (2) they establish polygynic and polydomic societies consisting of many thousands of individuals. Colonies are parcelled into sub-colonies (through seasonal "divisional migration" - Skaife, 1955; Markin, 1970; Benois, 1973) with nests established near food sources and permanent contact between sub-colonies maintained by means of trunk trails. Moreover, these nests are not permanent structures and may fuse with adjacent nests. Entire populations frequently move from area to area in response to unfavorable environmental conditions (food-source depletion, flooding, desiccation,...); (3) they perform massive and rapid recruitment mediated by odor trails, allowing them to respond quickly to local disturbances or the discovery of food.

Recent observations of *I. humilis* showed that exploration of new territories proceeds according to a well-defined behavior pattern. An ant column extends from the nest, then fans out at its distal extremity into a front of workers exploring individually in random directions. Whereas exploratory recruitment generally leads to the dispersion of ants on the new terrain, *I. humilis*' exploratory activity is a collective process, and resembles army ant
hunting raids, albeit on a smaller scale (Aron et al. 1989; Deneubourg et al. 1989a).

This paper will investigate how *I. humilis* exploits its territory at the colony level. This will involve territorial marking, the formation of exploratory trails, the discovery and exploitation of food sources, the formation of trails linking neighboring colonies and the selection of the shortest trails. These collective spatial patterns can be generated by simple interactions between a large number of identical explorers, through their trail laying and following behavior. This illustrates how complex structures may be based on self-organization processes.

EXPLORATORY BEHAVIOR

In order to study exploratory recruitment, a bridge was placed between the nest container and a chemically unmarked sand-filled arena (80 x 80 cm). The access of Argentine ants colonies to such unfamiliar terrain elicits an exponential outward surge of ants associated with collective exploratory behavior. The first workers entering the new arena individually explore, in random directions, the area closest to the nest. As this front progresses into the arena, a trail is formed which connects the front to the nest (Fig. 1a). In general, the larger the colony size, the faster the pattern formation, and the stronger the trail. For colonies above 1500 workers, the formation of more than one exploratory trail may occur. The rate of trail formation-progression is about two to three m/hour for a 600 ant colony. Some days later, the trail is still present, but no longer so well marked, with only a small number of foragers seen in the arena.

During recruitment, explorers returning to the nest move rapidly among quiescent nestmates, vigorously antennating them, and then return to the new

![Figure 1](image)

**FIGURE 1.** A) Collective exploratory pattern on a 80x80 cm. sand-filled arena after 20 min, colony of 600 workers. B) Idem, generated by Monte-Carlo simulation (see text). (from Deneubourg et al. 1989).
FIGURE 2. Percentage of ants per 3-minute period passing on the 2 branches of the bridge (insert). Colony of 1000 workers. (from Deneubourg et al. 1989).

terrain. Within seconds, stimulated workers leave the nest and begin trail-following. The occurrence of workers leaving the nest without any direct contact with recruiters suggests that the trail pheromone itself and/or the increased nest activity could be sufficient to induce recruitment.

Observation of explorers crossing the bridge between the nest and the new area showed trail-laying behavior both by those moving from and returning to the nest. The gaster was bent downwards and the ventral side dragged along the ground for varying lengths. The same behavior was reported by Van Vorhis Key and Baker (1986) during foraging recruitment. This strongly suggests that the same trail pheromone (Z-9-hexadecenal) is used during both food and exploratory recruitment. Z-9-hexadecenal was previously known to be a constituent of the ventral Pavan's gland secretion (Cavill et al. 1979, 1980) and its inducement of trail-following activity has been documented (Robertson et al. 1980; Van Vorhis Key and Baker, 1982a,b).

An analysis of video recordings suggests that workers crossing the bridge towards the nest lay significantly more pheromone than those moving in the opposite direction (Aron et al. 1989). They leave longer marks, with less distance between successive streaks. A theoretical study of the streak lengths' distribution showed that trail-laying approximates but is not a single-chain Markovian process.
GENERATION OF THE COLLECTIVE EXPLORATORY PATTERN

To study trail formation behind the exploratory front, the colonies were given access to a new sandy arena via a diamond-shaped bridge (Fig. 2, insert). This allowed a simple choice between one binary left/right path (in the arena, they have a much larger choice of directions). The dynamics of the ants' cumulative choice between both branches was then quantified. Initially, the flow of workers on both branches grows at a more or less equal rate. Soon, however, this symmetry is broken and one branch becomes more frequently used than the other (Fig. 2). The transition to an asymmetrical distribution can be considered the formation of the exploratory trail's latest segment at the trailing edge of the exploratory front.

Following an osmotropotactic trail-following model (Häntgartner, 1967; Pasteels et al. 1986), the workers' choice between the two branches may be a function of their relative pheromone concentrations. The more concentrated the pheromone on a branch, the more attractive for explorers, who also add to the pheromone concentration. Each passing ant modifies the following ant's probability of choosing left or right - positive feedback that, after initial fluctuation, rapidly leads to one of the two forks becoming completely preferred to the other.

This exploration on the bridge was modelled using two simplifications which do not influence the generated pattern (Deneubourg et al. 1989a). Firstly, it was assumed that the ants lay an equal quantity of pheromone when leaving or returning to the nest. Secondly, the pheromones' mean life-time may be estimated from previous data (Van Vorhis Key and Baker 1982a) as approximately 30 minutes. Its disappearance may therefore be ignored because plateau values are reached after 10-25 minutes in the experiments. This allows the quantity of pheromone laid on a branch (L and R) to be measured by the number of workers that have passed on that branch, independent of their direction.

Each ant at a choice point has a probability pl or pr of travelling along the left or the right branch, depending on the respective pheromone concentrations L and R, and adds one pheromone unit to the branch chosen. The unit for L and R is the average quantity of pheromone laid by an ant passing the choice point.

\[
pl = \frac{(k + L)n}{(k + L)n + (k + R)n}
\]

with \( pl + pr = 1 \), and \( L + R = \text{no. of previous ant crossings} \).

\( n \) is a coefficient of non-linearity: the higher \( n \), the higher the probability of choosing the more concentrated branch, even if there is only a slight difference between both branches. \( k \) represents the degree of an unmarked branch's "attractiveness": the greater \( k \), the greater the marking necessary for the choice to become significantly non-random. Figure 3 shows the results of 20 experiments on different colonies, with somewhat variable recruitment dynamics, as a function of the number of ant passages. The choice function (1) is fitted empirically by matching the experimental results with
FIGURE 3. Percentage of ants passing on the collectively selected branch of the diamond-shaped bridge. 20 experiments, 9 colonies of 150-1200 workers, measured every 3 minutes for 30 minutes (dots). 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 eq. (1) with n = 2, k = 20. (from Deneubourg et al. 1989.)

Monte-Carlo simulations based on this model (Fig. 3, dashed curve), giving n≈2 and k≈20.

Two dimensional exploration was simulated by extending the diamond-shaped bridge model to an interconnecting network of binary choices (Fig. 1b, insert). Two further working hypotheses were made. Since trailing ants move faster than those at the front, the probability of moving at each step increases sigmoidally with the pheromone quantity at the points ahead of the ant. Secondly, the explorers leave the nest, moving forward and then returning, according to a simplified logistic-type approximation of the observed recruitment dynamics. At each point the ants move and mark according to equation (1).

The 2-D simulation illustrated in Figure 1b reproduces the two major characteristics of the ants' exploration of a new area, namely the exploratory front and the exploratory trail. This shows how interactions between individuals, whose trail-laying and following behavior are reduced to their simplest expression, can generate the complex exploratory pattern.
Territorial Marking

During collective exploration the workers' trail-laying behavior in the exploratory zone probably constitutes a form of territorial marking, allowing the workers to know whether or not they are in a previously explored zone. The following classical series of experiments tested the relationship between exploration and territorial marking. Two sheets of paper (5 x 5 cm) were placed close to the nest entrance. At least one week later, one of them was replaced by a virgin, chemically unmarked paper.

The number of explorers on the virgin paper was significantly higher than on the familiar one, ants moved onto it more frequently than onto the familiar paper and stayed longer. This corresponds to definite "coming-and-going" behavior exhibited when the ants come across the virgin paper, as seen at the exploratory front during a collective exploration.

After some hours the activity on the virgin paper and the "coming and going" behavior progressively decrease. I. humilis workers thus appear to distinguish new areas from those previously explored, most probably by means of chemical cues. Preliminary results show that these territorial marks are long lasting, as familiar papers do not elicit increased exploratory activity even after one month's isolation.

Exploratory and Food Recruitment Trails

The use of the same recruitment trail pheromone both during foraging and exploration suggests a strong correlation between the two processes. I. humilis societies were starved four days before inducing successively exploratory and alimentary recruitments in a 2m² area. Once the exploratory pattern formed, a food source (1M sucrose) was introduced in the arena and the ants' movements followed for 20 min.

When placed about 20 cm from the exploratory trail, i.e. behind the exploratory front, the food was discovered by only a few foragers, and in many cases by none at all. Those that did find it generally left the food source and rejoined the exploratory trail, laying trail pheromone, but were unable to divert recruits to the food source from the much stronger exploratory trail.

When the food was placed 20 cm from the exploratory front, it was discovered more rapidly. Moreover, the discoverers rejoined the end of the exploratory trail, and directed exploratory recruits to the food source. The exploratory activity was replaced by exploitation of the food source and only a few scattered individuals continued exploration.

Although little is known about this behavior in nature, the number of ants participating in an exploration is probably larger than tested under laboratory conditions (about 600 ants/colony). In such a situation, the exploratory front would have to be large to discover and exploit any food present in the exploratory zone. Furthermore, there would have to be sufficient explorers to continue the collective exploration while also exploiting discovered food.

Short-Cuts

Unlike most ant species, which rely on a more highly developed individual capacity for orientation (review in Passera, 1984), the Argentine
ant's navigational information is characterized by strong collective communication: workers are integrated into a network of chemical trails which regulates their external activities. Can this collective process respond efficiently to environmental cues? Beckers et al. (1988) and Deneubourg et al. (submitted) have shown that an *I. humilis* colony (and other species) can indirectly select the richer of two food sources through mass recruitment. This study will show how *I. humilis'* permanent trail laying behavior allows its foragers to select collectively the shortest route between nest and food source (Goss et al. submitted).

Argentine ant colonies were given access to a food source (1M sucrose) via a bridge of two identical modules, each consisting of two branches of different lengths (Fig. 4). To minimize external factors, each module's short branch was placed on opposite sides of the bridge. Furthermore, a number of experiments were performed in the dark (under red light), i.e., with no visual cues whatsoever.

The first explorers cross the bridge and discover the food source. As the ensuing recruitment proceeds, bridge traffic increases, with workers travelling equally on both branches of the modules. However, just as described above during exploratory recruitment, one branch becomes progressively more exploited than the other during any given experiment. Which branch was chosen depended on how widely the ratio (r) of their lengths varied (r is the ratio of long branch to short branch length).

When the two branches were of equal length (r=1), one or the other branch of the bridge was chosen with about equal probability (12 times the left branch out of 26 tests). In three series of experiments, in which the two
branches were of different lengths, more than 80% of the foragers in more than 80% of the experiments selected the short branch \((r=2\) and \(r=1.4, 14\) and \(18\) tests respectively) as illustrated in Figure 4, even under red light \((r=2, 14\) tests). This last series shows that visual cues do not influence the ants' choice of the shorter branch.

Nevertheless, if the short branch is added only after a long branch trail is well-established, the trail's strength is such that in more than 80% of the tests the colony does not switch to the shorter branch \((r=2\).

The ants' selection of the shorter branch may again be modelled according to choice equation (1) (see model of exploration), taking into account the difference between the times the ants took to cross the bridge via the two different branches.

The workers which chose the short branch crossed it in approximately 20 seconds. Having laid pheromone at both ends of the bridge, they influence the choice of other workers going in both directions. Those that choose the long branch take 40 seconds \((with r=2\) to cross it. Thus while they immediately influence the ants following them, they only influence the ants crossing in the other direction 20 seconds later, i.e. 10 seconds more than an ant that chose the short bridge. Therefore, this slight difference initially favors the short branch, and is accumulated and amplified by the autocatalytic nature of the "choose and mark" process. The short branch soon becomes more or less completely preferred to the other.

Consider: one ant arrives at each of the two choice points \((j=1, 2)\) at each second. It chooses the short or the long branch with probability \(p_{s,j}\) or \(p_{l,j}\) depending on the respective quantities \(S_j\) and \(L_j\) of pheromone on the two branches. Having chosen, it adds one pheromone unit at the entry to the chosen branch. Twenty or 20r sec. later (depending on the branch chosen), it adds one pheromone unit to the exit point. The average equations are:

\[
dS_j/dt = P_{S,j}(t) + P_{S,j}(t-20) \quad \text{(2)}
\]

\[
j=1, j'=2 \text{ or } j=2, j'=1
\]

\[
dL_j/dt = P_{L,j}(t) + P_{L,j}(t-20r) \quad \text{(3)}
\]

\[
p_{s,j} = \frac{(20 + S_j)^2}{(20 + S_j)^2 + (20 + L_j)^2} \quad \text{(4)}
\]

Monte Carlo simulations of equations (2) to (4) give us two main results (Goss et al. submitted):

- the larger the difference between the short and the long branch, the greater the colony's probability of choosing the shorter branch;
- when the short branch is presented after the trail on the long branch has been established, the colony cannot switch to the short branch.

The model's results confirm that selection of the short branch is a collective decision, resulting from simple trail-laying and trail-following behavior. The model also predicts that another species whose workers only mark when returning to the nest (as in most ants species) would not select the shorter branch any more often than the long branch. In fact, the greater the
FIGURE 5. Four *I. humilis* colonies linked by four bridges arranged in a square setting up a network of communication (photos respectively taken 1 hr (5a) and 10 days (5b) after the bridges were placed). After a period in which all branches were used equally, only three branches were used in the long-term.
FIGURE 6. Schematic network of communication set up by three *I. humilis* colonies linked by 3 bridges arranged in an equilateral triangle (solid-lines). After rotation of 120° of the bridges, the same branches continue to be used (dashed-lines), now linking the colonies in a different way.

quantitative difference between marking by workers moving to and from the nest, the lower the probability that the colony will select the short branch.

**Network**

In most habitats colonized by the Argentine ant, nests are more or less evenly distributed. Each colony issued from springtime divisional migrations, nevertheless, remains connected to the others by a network of permanent trails. The workers, and more rarely some queens, move freely along these trails from one nest to the other. This behavior is also observed in the laboratory.

*I. humilis* colonies of about twenty to thirty thousand individuals were isolated from a common stock, each fed and watered extensively. They were connected by cardboard bridges. Two experimental devices were used: an equilateral triangle and a square with a colony at each apex. The ants' traffic on each branch of the bridge was measured every two days during the third week.

Initially, all branches of the bridge were frequented more or less symmetrically (Fig. 5a). With time, the exploration on the bridge decreases, and after two or three days an asymmetrical and permanent communication network appears (Fig. 5b). In all cases, the colonies remained inter-connected without using the most direct bilateral connections. In the triangular system, colonies 1 and 3 were linked via colony 2, and only two of the three branches used systematically. For the square, only three branches were used, colonies 1 and 4 connected via colonies 2 and 3 (Fig 5b).

When the experimenter broke one of the network's links, workers re-established a complete network by exploiting the previously less-frequented branch. Thus, a strong degree of plasticity allows the ants to maintain and connect all nests. Some preliminary experiments rotated the bridge but left the colonies as before. The ants, however, tended to maintain
the traffic on the same physical branches as before, although these now linked different colonies (Fig. 6). These findings strongly suggest that chemical rather than visual cues organize branch traffic.

However, while the configuration generated by the model using equation (1) was the same for the triangular set-up, the one generated for the square without diagonals is different from that seen in Fig. 5b and consists of colonies 1-2 and 3-4 linked, with each pair isolated from the other. Thus, although chemical marking clearly plays an important role in network establishment, another unknown factor intervenes that allows linkage of all the colonies. In each experimental case, the configuration adopted was the shortest network that still allowed each colony to be linked to the others. While a number of different configurations are currently being tested, this idea is reinforced by one case where four colonies were connected with a square, complete with diagonals. The ants used both diagonals, but not the sides of the square.

DISCUSSION

Iridomyrmex humilis' exploratory behavior is peculiar in that it is a collective activity that proceeds according to a well structured characteristic pattern in which the ants keep permanent contact with each other through the medium of chemical trails.

The genesis of a massive and collective exploratory behavior corresponds to their highly opportunistic and agonistic behavior. The chemical trails allow workers to return directly to the nest, leading to rapid mobilization of a large number of individuals to freshly discovered food sources and/or new sites. Furthermore, it constitutes a massive and permanent defense against other competing ant species, while ensuring territorial expansion.

As I. humilis reproduces by colony fission (budding) rather than aerial dispersal of queens (Newell, 1909; Newell and Barber, 1913; Skaife, 1955), collective exploration is also the major process ensuring the species' dispersion in the environment. Upon discovery of new sources or new nest sites by explorers, Argentine ant colonies split into "sub-colonies" of hundreds or even thousands of workers, some queens and brood, establishing different colonies near different food sources, and remaining inter-connected by the equivalent of trunk trails (Skaife, 1955; Markin, 1968, 1970; Dechène, 1970; Hölldobler and Wilson, 1977).

This communication network not only allows the exchange of workers, food, brood, queens, etc., between the nests, but also could constitute a useful means of maintaining territorial control (see also Hölldobler and Wilson, 1977, Hölldobler and Lumsden, 1980, Skinner, 1980, and Rosengren, 1985). Clear trails criss-cross the territory, connect different nests and help orient and rapid mobilize foragers. Between the trails, occasional foragers maintain a minimum degree of territorial marking while searching for food. This represents an efficient way for a large colony to maintain a large territory concentrating its exploitation on the most favorable sites and allowing a permanent and radial progression in all directions.

The probable use of the same pheromone (Z-9-hexadecenal) both in food and exploratory recruitment suggests that only one pheromone could be involved in the Argentine ants' spatial organization. Exploratory trails
become, with the discovery of food, food recruitment trails. These can then be used for moving the nest closer to resources. With time, and with the evaporation/deactivation of the (Z)-9-hexadecenal, these trails no longer recruit but remain as guidelines for territorial marking, and traffic between the different nests. If confirmed, this system is both elegant and economical.

The collective patterns discussed above are clearly self-organizing, involving a large number of simple interacting individuals coordinated by trail pheromone. One might expect that a similar permanent chemical network would appear in other large trail-laying social insect colonies. *I. humilis*’ exploratory behavior is also remarkably similar, on a smaller scale, to army ant-type exploratory/foraging “swarms” (Rettenmeyer, 1963; Topoff, 1972; Moffet, 1984, 1988; Franks and Fletcher, 1985), and the same basic model may be used for both (Deneubourg et al. 1989b). Highly similar exploratory patterns have been observed 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, pers. comm.).

The Argentine ant’s life-style, in particular its high reproductive rate, adaptability and rapid colonization of new territory, has much in common with other well-known pest species such as *Solenopsis* sp., *Tapinoma melanocephalum* or *Monomorium pharaonis.*

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