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Self-organized Shortcuts in the Argentine Ant

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It is evident that finding the shortest route is extremely important not only for Roman road builders, thirsty rugby men and applied mathematicians working on this very problem, but also for any animal that must move regularly between different points. How can an animal with only limited and local navigational information achieve this? Many ant and epigeic termite species illustrate this problem in the clearest possible way. The individual workers are generally less than 1 or 2 cm long, and must cover distances of 1 to 100 m between their nest and food sources. Even those that are capable, by visual or other means [1], of returning in a straight line to the nest are confronted with innumerable obstacles in their path that form a labyrinth worthy of the Minotaur. The Argentine ant *Iridomyrmex humilis* studied in this article has only a limited individual capacity for orientation [2], yet we shall see how by interacting with each other via their trail pheromone, they are capable of selecting with great reliability the shortest route between nest and food.

Laboratory colonies of *I. humilis* are given access to a food source in an arena linked to the nest by a bridge (Fig. 1), consisting of two identical modules. Each module has two branches of different lengths, arranged

such that a forager going in either direction (leaving the nest or leaving the food) must choose between one or the other (at choice points 1 and 2, respectively). Each branch is at an angle of 30° to the axis of the central bridge, so that the forager has no preference for one or the other branch due to its disposition. This value of 30° has been chosen to minimize the perturbation to the forager's movement, so that on leaving one or the other branch they continue rather than double back onto

the other branch. To examine if any external bias is involved, one module's short branch is on the opposite side of the bridge as the other.

Five to 10 min after placement of the bridge, explorers have crossed it and discovered the food. Food recruitment then adds to the exploratory recruitment, and traffic on the bridge increases, the foragers at first choosing equally between the short and long branch of both modules. Abruptly, some minutes later, one branch becomes visibly preferred (Fig. 1b,c).

Knowing that *I. humilis* workers mark both leaving and returning to the nest, during food [3] and exploratory [2] recruitment, we model the behavior on the bridge as follows. Φ ants cross the bridge in each direction per second, each laying one pheromone unit. Arriving at one of the choice points ($j=1,2$) of a module, each ant chooses the short or the long branch with probability $p_{s,j}$

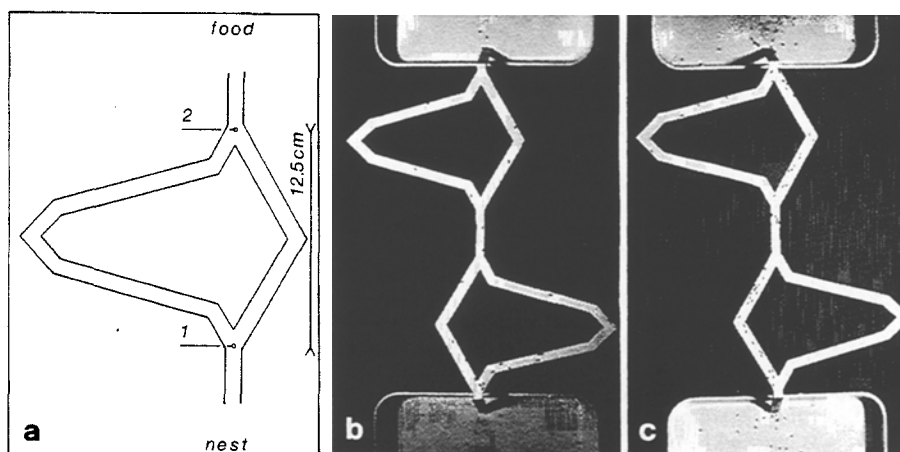


Fig. 1. A colony of *I. humilis* selecting the short branches on both modules of the bridge; a) one module of the bridge, b) and c): photos taken 4 and 8 min after placement of the bridge

or $p_{1,j}$, depending on the quantities S_j and L_j of pheromone on the two branches at that choice point, and then adds to the pheromone on the branch chosen. Those that choose the short branch at $j=1$ (or 2) arrive at the opposite choice point $j=2$ (or 1) approximately 20 s later, given their average speed and the length of the short branch, and add to the pheromone there. Those that choose the long branch do so $20r$ seconds later, where r is the ratio of the length of the long branch to the short one. The time scale of these experiments is of the order of the mean lifetime of the pheromone (≈ 30 min) [4], allowing us to ignore the evaporation of the pheromone. Thus, at time t , the average equations for this stochastic system are:

$$dS_j/dt = \Phi p_{s,j'}(t-20) + \Phi p_{s,j}(t) \quad (1)$$

($j=1, j'=2; j=2, j'=1$)

$$dL_j/dt = \Phi p_{l,j'}(t-20r) + \Phi p_{l,j}(t) \quad (2)$$

$$p_{s,j} = \frac{(20 + S_j)^2}{(20 + S_j)^2 + (20 + L_j)^2} \quad (3)$$

($p_{s,j} + p_{l,j} = 1$)

Eq. (3) is the choice function based on our previous experimental study [5] in which we showed how, faced with a

choice between two equal paths during an exploratory recruitment, each ant that passes the choice point modifies the following ant's probability of choosing left or right by adding to the pheromone on the chosen path. This positive feedback system, after initial fluctuation, rapidly leads to one branch being "selected".

The delays in Eqs. (1) and (2) are of course the key to how the ants choose the short branch, as they lead to an initial period in which the short branch at both choice points is marked by the ants moving in both directions while each choice point of the long branch is only marked by ants moving in one direction. Consider the choice point nearest the nest. At time 0 it is unmarked. The first ants arrive, choose randomly and travel along their chosen branch, marking as they go. After 20 s, however, the short branch will be marked not only by fresh ants arriving from the nest, but also by the first ants returning to the nest that chose the short branch. This happens only later for the long branch, i.e., after $20r$ s. Between these two moments, the short branch accumulates an advantage over the long branch at both ends. This is amplified by the autocatalytic nature of the

choose-and-mark process, and the short branch rapidly becomes preferred unless random noise reverses the advantage. The greater the initial advantage, i.e., the greater Φ and the difference between the two branches, the more probable it is that the short branch is chosen.

What does the model predict? Firstly, the colony's probability of selecting the shortest branch increases with the difference between the two branches, as seen from the Monte Carlo simulations summarized in Fig. 2a-c. For two equally sized branches ($r=1$), one of the two is randomly selected (Fig. 2a).

Secondly, if the short branch is only present after the trail on the long branch has been established, the colony should be incapable of switching to the short branch, due to the irreversible nature of the positive feedback process involved, as seen from the Monte Carlo simulations summarized in Fig. 2d.

Thirdly, if, as for most ant species, the workers only mark when returning to the nest, it is easy to understand that in this case it is not possible for the colony to select the shortest branch more often than the long branch, as there is no initial period during which the short branch is marked twice as much as the

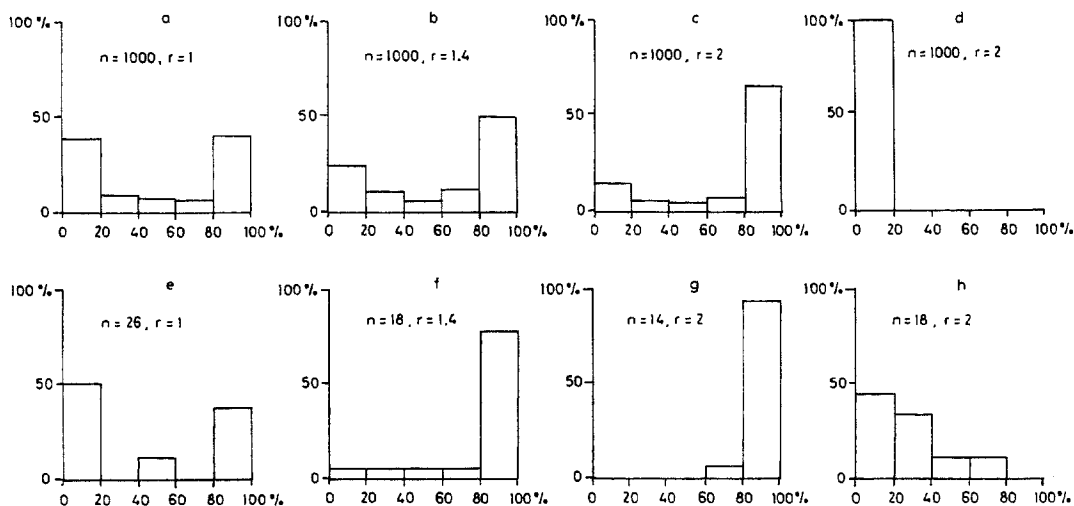


Fig. 2. The distribution of ants that chose the short branch (r = ratio of long branch length to short branch, n = no. of trials). Monte Carlo simulations, with $\Phi=0.5$ ant s^{-1} , traffic ($\Sigma\Phi$) counted between the 501st and 1000th ant crossing the bridge: a) $r=1.0$, $n=1000$, $\Sigma\Phi=500$, b) $r=1.4$, $n=1000$, $\Sigma\Phi=500$, c) $r=2.0$, $n=1000$, $\Sigma\Phi=500$, d) $r=2.0$, $n=1000$, $\Sigma\Phi=500$ (short branch added after 1000th crossing, traffic counted between 1501st and 2000th crossing). Experiments were performed on 11 different *I. humilis* colonies. Traffic was counted between 30th and 40th min after placement of the bridge (Fig. 1): e) $r=1.0$, $n=26$, $\Sigma\Phi=425-1043$ (as $r=1$, short branch = the branch on the left leaving the nest), f) $r=1.4$, $n=18$, $\Sigma\Phi=329-696$, g) $r=2.0$, $n=14$, $\Sigma\Phi=407-912$, h) $r=2.0$, $n=18$, $\Sigma\Phi=317-846$ (short branch added 30 min after the experiment began, traffic measured between 20 and 30 min later). For the smallest total traffic ($\Sigma\Phi=317$), the choice is significantly nonrandom if the ants choosing a branch are outside the range 44–56% ($p<0.05$)

long. More generally, the greater the difference between the marking made by the ants leaving the nest and that by those returning to the nest, the more random is the overall choice between the two branches.

The experiments summarized in Fig. 2e–g confirm the first prediction (cf. Figs. 2a–c). When the two branches were equal ($r=1$) no significant overall preference was noted (12/26; $p > 0.05$). With $r=1.4$ and $r=2$, the ants showed a significant and increasing overall selection of the short branch (15/18 and 14/14, respectively; $p < 0.05$).

When the short branch was added only after the trail on the long branch was established (Fig. 2h, $r=2$) the ants were unable to switch to the shorter branch (2/18; $p < 0.05$), confirming the second prediction (cf. Fig. 2d). The third prediction is currently being tested.

It is important to note that the selection of the shortest branch is not the result of individual ants comparing the different lengths of each branch, but is instead a collective and self-organizing process, resulting from the interactions between the ants marking in both directions. We have deliberately neglected any possible effect of individual memory so as to present the simplest possible explanation for this capability. While memory or other factors might intervene, their role is not an essential one.

This approach is supported by the following experiments. To test the influence of visual cues, the experiments described in Fig. 2g were also carried out under red light to which ants are insensitive (i.e., in the dark). The results were not different from those performed in light. In 11 of 14 experiments ($r=2$, 7 different colonies), more than 80% of the total traffic used the short branch.

To test the possible existence of a spatial left/right memory which might contribute to (or interfere with) the selection of the short branch, three experiments were performed with a Y-shaped bridge. This had one fixed branch (the base of the Y) connected to the nest entrance and two replaceable branches (the fork of the Y) leading to a foraging arena and diverging from each other at an angle of 60°. Foragers were at first given access to a food source placed at the end of one of the

branches (left or right), and were marked with a drop of paint while feeding. After 10 min the two replaceable branches were replaced by new, unmarked ones. We then recorded the choice of each worker (marked and unmarked) passing over the bridge during the next 10 min. Once having crossed the bridge and reached the foraging arena, they were immediately removed and kept apart until the end of the experiment. Summing the results of the three experiments, the marked ants chose more or less equally between both unmarked branches, i.e., did not automatically choose the unmarked branch that led to the food (16 chose the branch that led to the food vs 12 that chose the other branch). This suggests that left/right memory is not important in the workers' spatial orientation in such situations. Various other data also indicate the predominance of chemical cues in this species' orientation.

Finally, over all the experiments, the selection of the short branch was independent of whether it was on the left or on the right when leaving the nest. The results obtained by those colonies which were used for more than one trial do not differ when one compares the first trial to the second one, indicating that experimental replications do not increase a colony's capacity for selecting the short branch.

With these results we can predict that any ant or termite species that reinforces its trail in both directions or marks permanently can select shortcuts (e.g., *Pheidole militica* [6], *Solenopsis* spp. [7], *I. pruinosus* [8], *Eciton* spp. [9], *Trinervitermes geminatus* [10], *Pogonomyrmex badius* [11], *Leptogenys* spp. [12]). Finding a short route is especially important for epigeic termites as they must invest in the construction of a gallery around the trail.

We have previously shown how such simple and permanent trail-laying and trail-following behavior is also the principal factor behind the organization of the collective exploration [5] and spatial organization [2, 13] of *I. humilis*, as well as the complex foraging patterns seen in group-raiding species such as army ants and termites [14]. It is increasingly clear that many social insects achieve complex and adaptive foraging behavior by integrating a large number of simple foragers into a per-

manent network of pheromone communication. Unlike other social insects which rely on a more highly developed individual capacity for learning and orientation, the source of their complexity may be said to lie in the interactions between their workers.

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