

Path selection and foraging efficiency in Argentine ant transport networks

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Abstract We experimentally investigated both individual and collective behavior of the Argentine ant *Linepithema humile* as they crossed symmetrical and asymmetrical bifurcations in gallery networks. Ants preferentially followed the branch that deviated the least from their current direction and their probability to perform a U-turn after a bifurcation increased with the turning angle at the bifurcation. At the collective level, colonies were better able to find the shortest path that linked the nest to a food source in a polarized network where bifurcations were symmetrical from one direction and asymmetrical from the other than in a network where all bifurcations were symmetrical. We constructed a model of individual behavior and showed that an individual's preference for the least deviating path will be amplified via the ants' mass recruitment mechanism thus explaining the difference found between polarized and non-polarized networks. The foraging efficiency measured in the simulations was three times higher in polarized than in non-polarized networks after only 15 min. We conclude that measures of transport network efficiency must incorporate both the structural properties of the network and the behavior of the network users.

Keywords Transport networks · Argentine ant · *Linepithema humile* · Path selection · Bifurcation geometry · Foraging efficiency

Introduction

Transport networks play a crucial role in the distribution of materials and information at all scales both in natural and man-made systems. Many such networks have been studied during the last 10 years, for example, the internal 3D vascular systems of plants and animals (West et al. 1997, 1999a, b; Banavar et al. 1999, 2002), the external 2D road networks built by human societies (Buhl et al. 2006; Gastner and Newman 2006), and the shape of transport networks in the true slime mold *Physarum polycephalum* (Nakagaki et al. 2004a,b) and in fungi (Bebber et al. 2007). Among the most striking examples of biological transport networks are those created by social insects. The nests of termites and ants for instance are typically composed of several chambers interconnected by a network of galleries that exhibit species-specific architectures (Darlington 1997; Cassill et al. 2002; Tschinkel 2003; Mikheyev and Tschinkel 2004; Perna et al. 2008). Outside the nest, some species of ants build dendritic networks of chemical and/or physical trails that radiate out from the nest and that are used during the exploration of their environment or while they exploit food sources (Anderson and Mcshea 2001).

Recent studies on transport networks in social insects have mostly focused on network structure and measured the topological and/or geometrical relationships between the components of the network in order to identify its structural invariants or to estimate its efficiency and robustness. For instance, Perna et al. (2008) have shown that nests of *Cubitermes* termites display an excellent compromise between efficient connectivity within the nest and defense against predators from outside the nest. In the ant *Messor sancta*, Buhl et al. (2004) showed that the gallery networks achieve a near optimal compromise between a highly efficient network and a highly robust one. Less is known,

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however, about the way insects use their transport networks and how they distribute themselves within the network, for instance, when they travel within the subterranean network of their nest or within a foraging network on the surface. Yet the efficiency of a transport network depends directly on the way a network is used.

While moving within their networks, ants often lay down a pheromone trail that is followed by other ants that in turn lay down additional pheromone deposits thus attracting more ants. At a given bifurcation in a network, this positive feedback may eventually lead to most traffic focusing on one single branch (Deneubourg and Goss 1989) if certain conditions of traffic and ant density are met (Dussutour et al. 2004). In species where individuals are mainly guided by pheromone trail and do not use environmental cues to orient themselves, any error at one bifurcation will propagate over the following bifurcations and ants may eventually get trapped into sub-optimal pathways or network loops (Sumpter and Beekman 2003).

One solution for ants to navigate efficiently within their networks would be to use polarized trails that could indicate to the workers whether they are walking away from or going back to their point of departure. It has recently been suggested that the geometry of the bifurcations in a network could act as such a polarization cue (Jackson et al. 2004). Indeed, it has been shown that, in foraging trail networks, the mean angle between trail bifurcations as they branch out from the nest is 50° – 60° (*Atta sexdens*, *A. capiguara*, *A. laevigata*, and *Messor barbarus*=Acosta et al. (1993); *Monomorium pharaonis*=Jackson et al. (2004); *Formica aquilona*=Buhl et al. (2009)). Therefore, an ant exiting the nest and moving to food sources located at the periphery of the network generally faces symmetrical bifurcations, i.e., the two trails that follow a bifurcation deviate by approximately 30° from the ant's original direction. An ant coming back to its nest on the other hand faces asymmetrical bifurcations: at a bifurcation, the trail leading to the nest that follows the bifurcation deviates less ($\sim 30^{\circ}$) from the ant's original direction than the other trail ($\sim 120^{\circ}$) that leads away from the nest. Jackson et al. (2004) showed that when unfed *M. pharaonis* ants face an asymmetrical bifurcation, they have a high tendency to make a U-turn and return to their point of departure. Fed ants on their way back to the nest do the same when they face a symmetrical bifurcation. Therefore, *M. pharaonis* ants use the geometry of the bifurcation to orient themselves correctly within the network.

In the Argentine ant *Linepithema humile*, Gerbier et al. (2008), using artificial gallery networks, showed that workers that return to the nest with food and reach an asymmetrical bifurcation preferentially select the path that deviates less from their current heading and perform more U-turns on the path that deviates more. As a consequence,

the less deviating path should be marked with a greater amount of pheromone and should be more likely to be selected by ants. Because this path is more likely to lead to the nest in natural networks, one would expect that an Argentine ant colony should be more prone to select the most direct path between a food source and its nest. Moreover, one would expect that a colony would lose this ability if the workers only encounter symmetrical bifurcations.

In this paper, we test the above hypothesis by performing experiments both at the individual and the collective level. We assess the global behavior of Argentine ant colonies when given access to two relatively complex artificial networks of galleries in which several possible interconnected paths can lead the ants from their nest to a food source. The first network presents a polarized geometry: the bifurcations are symmetrical from one direction and asymmetrical from the other. Conversely, the second network is not polarized: the bifurcations are symmetrical from every direction. We also observe and quantify the behavior of ants while they cross a bifurcation in the polarized and the non-polarized networks. Based on our observations, we then build an individual-based model of the ants' behaviors to investigate the link between the individual behavior of ants at bifurcations, their trail-laying and trail-following abilities, and the global behavior of the colony in the two networks. The model also helps us to estimate and to understand the foraging efficiency of the colony in each type of network.

Materials and methods

Biological material

We used colonies of the Argentine ant *Linepithema humile* (Formicidae, Dolichoderinae) collected near Narbonne on the French Mediterranean coast. At this location, the Argentine ant is considered an invasive species and is unicolonial (the species forms a gigantic colony extending along the Mediterranean coast from Italy to Portugal and individuals mix freely among physically separated nests; Giraud et al. 2002). Ants were housed in artificial plaster nests ($\varnothing=10$ cm) without queen or brood and had access to an external foraging area. Twenty nests containing 2,000 workers each were used to study individual behavior and 20 nests containing 500 workers were used to study collective behavior. The ants were reared in an experimental room at a constant temperature of 25°C under L:D 12:12 conditions and fed twice a week with a mixture of eggs, carbohydrates, and vitamins (Bhatkar and Whitcomb 1970) and with *Musca domestica* maggots. The colonies were starved for 3 days before each experiment.

Individual behavior

Individual behavior of the ants at bifurcations was investigated in a series of alternatively inverted Y-mazes (see Fig. 1, left). The PVC plate in which the mazes were carved could slide between two other PVC plates that were fixed. A transparent PVC plate fixed on the two lateral plates covering the whole setup prevented the ants from escaping the maze. Small access galleries were carved in one of the two fixed plates, while in the other fixed plate small circular chambers ($\varnothing=20$ mm), each with a 15-mm-long and 5-mm-wide access gallery, were carved. The depth of the galleries and chambers was 5 mm. During a test, the central plate of the setup was slit so that each branch of a maze coincided with one access. To prevent the use of external visual cues, the whole setup was surrounded by a white sheet, which also ensured an indirect and diffuse lighting.

We tested the ants' behavior in two different types of Y-mazes: polarized mazes (P-mazes, Fig. 1, top left) and non-polarized mazes (NP-mazes, Fig. 1, bottom left). In P-mazes, the angle between the three branches was not the same. According to the position of the access branch, an ant could face either a symmetrical (each exit branch deviates by 30° from the access one) or an asymmetrical bifurcation (one exit branch deviates by 30° while the other deviates by 120° from the access branch). In NP-mazes, the angle between the three

branches was the same. Whatever the position of the access branch, an ant faced only symmetrical bifurcations with each exit branch deviating by 60° from the access branch.

In each type of maze, ants were tested successively in a single trip from the nest to the source (unfed ants, foodbound trip) and in a single trip from the source to the nest (fed ants, nestbound trip). Each ant was tested once and was excluded from the experimental colonies after being tested. In P-mazes, four situations were tested: S–A (foodbound trip with symmetrical bifurcation S and nestbound trip with asymmetrical bifurcation A), S–S, A–S, and A–A. When ants were tested with a different type of bifurcation in their food- and nestbound trips (S–A and A–S), the same maze was used. When they were tested with the same type of bifurcation on both trips (S–S and A–A), two adjacent mazes were used: the sliding part of the experimental setup was moved to a new maze while the ant was drinking in order to offer the same type of bifurcation during the foodbound trip and the nestbound trip. Fifty ants were tested in each situation, which allowed us to observe 100 unfed ants crossing a symmetrical bifurcation, 100 unfed ants crossing an asymmetrical bifurcation, 100 fed ants crossing a symmetrical bifurcation, and 100 fed ants crossing an asymmetrical bifurcation. In NP-mazes, two situations were tested: unfed ants and fed ants. Fifty-five ants were tested in each situation.

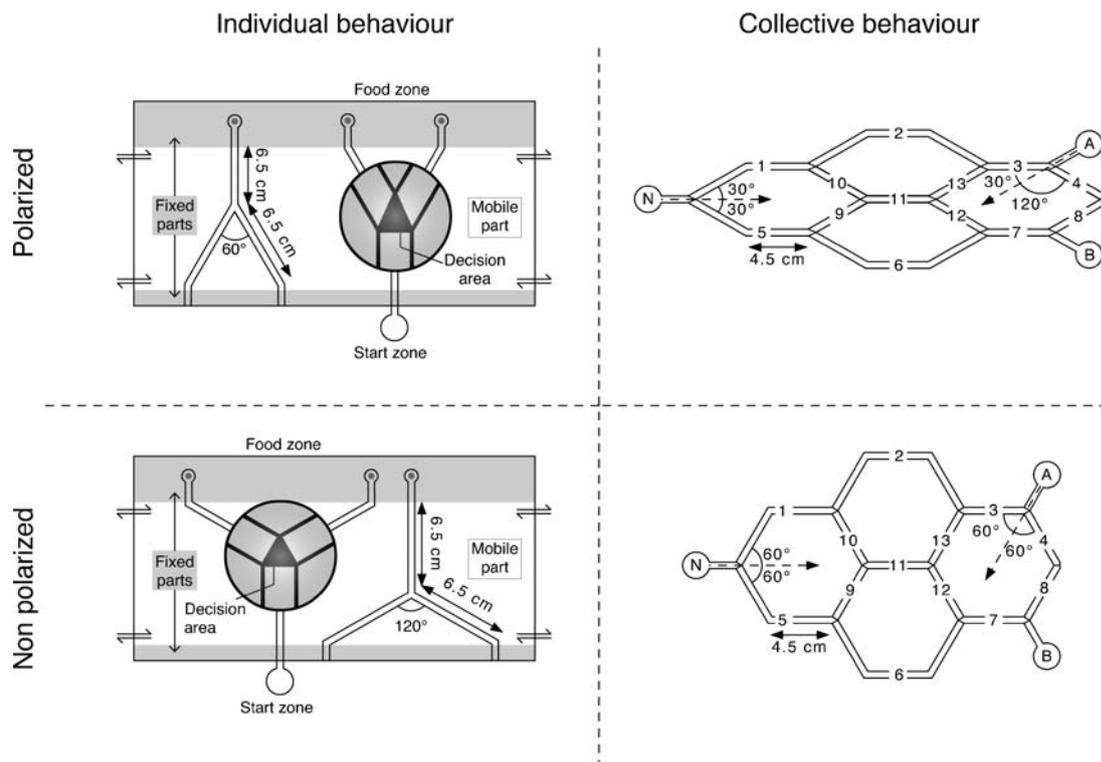


Fig. 1 Schematic representation of the experimental setups. *Left*: experimental setups for testing the individual behavior of the ants at a bifurcation. *Right*: experimental setups for testing the collective behavior

of the ants in a network of galleries. *Top*: polarized condition (P-mazes). *Bottom*: non-polarized condition (NP-mazes). *N* corresponds to the nest, and *A* and *B* to the chambers in which the food was placed

A test started by collecting an ant in the foraging area of its colony. A small wooden stick was introduced in the foraging area until an ant spontaneously climbed up and explored it. The ant and the wooden stick were then gently moved towards a small Petri dish placed in front of an access gallery. During this short displacement (no more than 50 cm), we took care not to touch the ant exploring the stick. To release the ant into the Petri dish, we allowed the ant to walk down spontaneously by placing one end of the stick onto the bottom of the dish. Finally, the ant explored the Petri dish for at least 1 min. All these precautions were taken to reduce disturbances caused by the moving of the ant. A food source (a small piece of cotton soaked with a 1 M solution of sucrose) was placed in each circular chamber (during symmetrical foodbound tests) or in only one of them (during asymmetrical foodbound tests). We waited until the ant found the food source and, after it had fed on it, until it went back to its point of departure. For each situation, the following data were recorded:

- Initial choice: the first branch chosen after the ant crossed the bifurcation for the first time. A branch was considered as chosen when the ant reached and moved beyond an area we called “decision area” (see Fig. 1, left). Note that, in rare cases (eight cases over 510 tests), an ant could enter the decision area and make a U-turn to go back toward its point of departure. In that case, the initial choice of the ant was not taken into account.
- Whether or not the ant made a U-turn on the branch chosen after crossing the bifurcation for the first time. Spontaneous U-turns occurring before an ant reached the bifurcation for the first time were not considered.

For each of the six experiments, pieces of paper on which a fresh chemical trail had been deposited were placed at the bottom of the maze galleries prior to the experiment. To avoid the effect of trail decay, the same pieces of papers were used during only 20 min (the trail pheromone duration of *L. humile* is estimated to be close to 30 min according to Deneubourg et al. (1990)). This allowed us to test on average three ants. The six pieces of paper (three for the access galleries and one for each branch of the maze) that were used to cover the bottom of the maze were cut from a piece of paper that had been marked during 30 min by workers of another colony moving between their nest and a food source (1 M solution of sucrose). This duration was sufficient to ensure that the paper was marked homogeneously.

If ants lay down a trail during their outbound trip, they could theoretically use it during their return trip when the same maze is used. However, added pieces of paper were saturated by trail pheromone and it seems highly unlikely that ants could be able to perceive their own trail against this background to orient on it during their return trip. When

two adjacent mazes were used, the pieces of paper that were placed in the two mazes were marked by two different experimental colonies. Since the Argentine ant is unicolonial (Tsutsui et al. 2000; Giraud et al. 2002), workers of one colony readily follow a trail laid by another colony.

Collective behavior

The ants’ collective behavior was tested in a maze carved in a PVC plate. The maze was composed of four identical hexagons assembled together (see Fig. 1, right). We tested the ants’ collective behavior both in polarized (P-mazes, Fig. 1, top right) and non-polarized mazes (NP-mazes, Fig. 1, bottom right). In NP-mazes, the six angles of each hexagon were equal to 120°. As a consequence, all the bifurcations in the network were symmetrical: at a bifurcation, each branch deviated by a 60° angle from the other two. In P-mazes, two of the six angles of each hexagon (the closest from the nest and the closest from the food source) were equal to 60°, while the other four were equal to 150°. As a consequence, all the bifurcations were symmetrical from one branch and asymmetrical from the other two.

Each maze also included an entrance gallery connected to the nest of an ant colony and two circular chambers ($\varnothing=20$ mm, A and B on Fig. 1, right) in which food (a piece of cotton soaked with a 1 M solution of sucrose) could be placed. The maze galleries had a 5-mm square section. The whole setup was surrounded by a white sheet to prevent the use of any directional cues by the ants and to ensure an indirect and diffuse lighting. A transparent PVC plate covering the whole maze prevented the ants from escaping. Ten of the experimental colonies were tested in P-mazes while the other ten were tested in the NP-mazes. For half of the colonies in each type of mazes, the food source was located in one chamber and for the other half, in the other chamber. Experiments with P-mazes and NP-mazes were alternated to randomize a potential effect of uncontrolled climatic variations (such as pressure or seasonal effect for instance). An experiment began when the first ant entered the network and then lasted 15 min.

The whole experiment was recorded continuously with a standard definition digital camera (Sony CDR-VX 2000 E) placed above the setup. We extracted one frame per second from the video recording plus one reference image of the network while it was empty. For each extracted frame, we computed the gray level difference between each pixel and the corresponding pixel in the reference image. If the absolute value of this difference was superior to a given threshold (here fixed to 30), the pixel was turned black. Otherwise, it was turned white. We then counted the number of black pixels in each segment of the network. A segment corresponds to a gallery linking two successive bifurcations. For each experiment, we estimated the mean

number of pixels covered by one ant by counting the number of black pixels and the corresponding number of ants on 13 different frames picked up every 70 s. From this, we computed the number of ants present in each segment of the network for each second of the experiment and we applied a moving average over a period of 30 s to reduce the noise introduced by the picture analysis process.

For each type of maze we computed the following:

- Mean number of ants in the network as a function of time.
- Mean number of used segments as a function of time. A segment is considered as used if the density of ants is superior to $0.22 \text{ ants cm}^{-1}$.

For a given frame, we also specified the path selected by ants as follows. We followed the segment with the highest density of ants, starting from each network bifurcation, until we reached either a bifurcation followed by two empty segments or a previously visited bifurcation or the food source. If we reached a bifurcation followed by two empty segments, we allocated this path to the “no path” category. If we reached a previously visited bifurcation, we allocated this path to the “loop” category. There are 14 possible paths to reach the food source without using the same segment twice. We classified the paths selected by the ants to reach the food source according to their length: 27, 36, 45, 54, and 63 cm. By repeating this process on each frame of each experiment, we obtained the time sequence of path selection events. We then grouped all consecutive frames that showed the same path category into a single event that was called a selection event. We then computed the following data for each type of maze:

- Mean number of selection events.
- Mean duration of selection events for each selected path category.

Experimental results

Individual ant behavior

Initial choice

There was no significant difference in the performance of fed and unfed ants (Fisher exact test— $P=0.367$, $P=0.396$, and $P>0.99$, respectively), regardless of whether the ants crossed an asymmetrical bifurcation or a symmetrical bifurcation in either the P-mazes or NP-mazes. We therefore pooled the data for foodbound and nestbound ants for the three types of bifurcation tested.

At the symmetrical bifurcation of P-mazes and NP-mazes, ants chose equally between the two branches that

followed the bifurcation (P-mazes=103 ants chose the right branch and 96 ants chose the left; NP-mazes=51 right and 59 left; binomial test— $P=0.671$ and $P=0.505$, respectively). At the asymmetrical bifurcation of P-mazes, however, ants expressed a significant preference in their initial choice for the branch that deviated by an angle of 30° over the branch that deviated by an angle of 120° (126 ants chose the 30° branch and 66 chose the 120° one; binomial test— $P<0.001$). The proportion of ants that selected the branch that deviated by an angle of 30° was 0.66.

U-turns

The proportion of ants making a U-turn after crossing a symmetrical bifurcation was not statistically different between the two branches that followed the bifurcation and between foodbound and nestbound ants in both P-mazes and NP-mazes (Cochran–Mantel–Haenszel exact conditional test of independence in $2 \times 2 \times k$ contingency tables; Agresti (2002)— $P=0.368$ and $P=0.845$, respectively). We therefore pooled the data for the two branches and for the foodbound and nestbound ants for the symmetrical bifurcations of P-mazes and NP-mazes, respectively. A significant difference was found between P-mazes and NP-mazes for the proportions of ants making a U-turn after crossing a symmetrical bifurcation (22 out of 199 ants performed a U-turn in P-mazes and 35 out of 137 in NP-mazes; Fisher exact test— $P=0.007$). While these two kinds of bifurcations are symmetrical, they deviated from the original direction of the ants by a different angle (30° in P-mazes and 60° in NP-mazes). This indicated that the proportion of U-turns is related to the angle between the former and the new direction followed by the ants.

In the asymmetrical bifurcations of the P-mazes, there was no statistically significant difference between foodbound and nestbound ants for the branch that deviated by an angle of 30° and for the branch that deviated by an angle of 120° (Fisher exact test— $P>0.99$ and $P=0.218$, respectively). However, the proportion of ants making a U-turn was significantly dependent on the angle by which the branch deviated (12 out of 127 ants performed a U-turn in the 30° branch and 38 out of 67 in the 120° one; Cochran–Mantel–Haenszel exact test— $S=12$, $P>0.001$).

In P-mazes, no significant difference was found in the proportion of U-turns between ants crossing a symmetrical bifurcation (and deviating from their original direction by an angle of 30° , 22 out of 199 ants) and ants choosing the branch that deviated by an angle of 30° in an asymmetrical bifurcation (12 out of 127 ants). As mentioned previously, this indicated that the proportion of U-turns is related to the angle between the former and the new direction followed by the ants. We therefore pooled the data for 30° deviations in symmetrical and asymmetrical bifurcations in P-mazes.

After all data pooling had been done, we finally computed the proportion of ants making a U-turn after a deviation of 30°, 60°, and 120° and we obtained 34 out of 326 (≈ 0.10), 35 out of 137 (≈ 0.26), and 38 out of 67 (≈ 0.57), respectively.

Collective behavior

General network use

The mean number of ants in the network at each time frame followed a sigmoidal growth for both P-mazes and NP-mazes (Fig. 2a). However, while the value in P-mazes reached a plateau around 40 ants, in NP-mazes it increased up to 60 ants (two-sample Student test over the last minute of experiment, $t=-2.3385$, $df=16.921$, $P=0.0319$). Each tested colony was randomly assigned to a type of maze and P-mazes and NP-mazes were tested alternatively. Thus, the numbers of ants involved in the exploration of the environment at the start of the experiments were likely to be equivalent between the two types of mazes. This is confirmed by the first 300 seconds of the experiments where the numbers of ants in P-mazes and NP-mazes were indistinguishable (two-sample Student test over the first 5 min of experiment, $t=-0.5269$, $df=17.672$, $P=0.6048$).

The mean number of used segments followed the same general dynamics (Fig. 2a, inset). It also displayed a quantitative difference between the two types of mazes, the mean number of used segments being higher in NP-mazes than in P-mazes in the second half of the experiments (two-sample Student test over the last minute of experiment, $t=-2.5746$, $df=11.731$, $P=0.0247$). Therefore, ants were less dispersed in P-mazes than in NP-mazes.

Path selection

A significant difference was found between P-mazes and NP-mazes in the mean number of selection events (15.2 ± 2.1 vs. 33.4 ± 4.9 , two-sample Wilcoxon test with continuity correction, $W=14.5$, $P=0.008$). In P-mazes, the number of selection events was lower than in NP-mazes; once ants selected a path in P-mazes, they were less likely to switch to another path than ants in NP-mazes (Fig. 3a, inset). Moreover, a two-way ANOVA revealed a significant difference between the different path categories ($F_{6,72}=14.326$, $P<0.001$) and between the two types of mazes ($F_{1,72}=10.935$, $P=0.002$) for the mean duration of a selection event, and a significant interaction between these two factors ($F_{4,72}=3.662$, $P=0.009$). In particular, when ants in P-mazes selected a shorter path (one of the 27-cm paths), they used it for a significantly longer time than ants in NP-mazes (Tukey HSD test, $P<0.001$; see Fig. 3a).

Model

Our model is a modified version of the model used in Vittori et al. (2006).

Model description

According to Camazine et al. (2001), the flow of ants leaving the nest and entering the network at each time step can be modeled as follows:

$$F_{\text{entrance}} = \frac{k_0(k_1 + C_{\text{entrance}})^m}{k_2 + (k_1 + C_{\text{entrance}})^m}$$

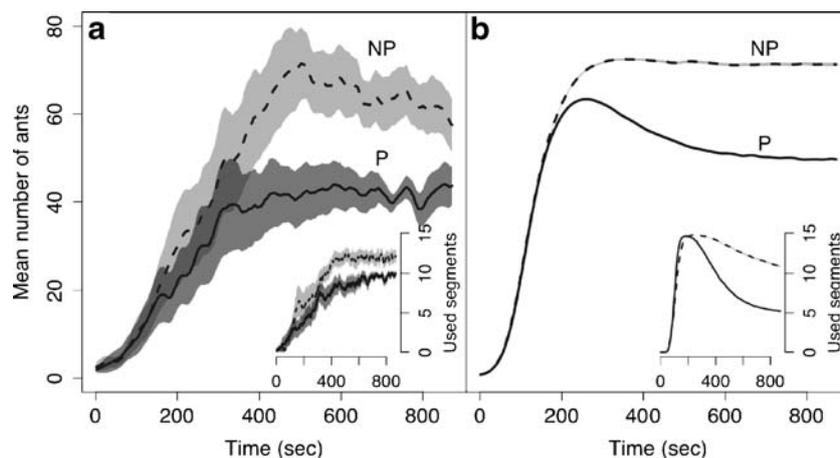


Fig. 2 Mean number of ants in the network (*main figures*) and mean number of used segments (*insets*, density of ants superior to 0.22 ants cm^{-1}) as a function of time. **a** Experimental results ($n=10$). **b** Simulation results ($n=1,000$). *Plain curves* represent data for polarized

networks. *Dashed curves* represent data for non-polarized networks. Each *curve* represents the mean \pm standard error (*light and dark gray polygons*). Note that the standard errors for the simulation results are too small to be seen

C_{entrance} corresponds to the total quantity of pheromone deposited by the ants at the entrance of the network; k_0 regulates the maximal number of ants that can enter the network at each time step; k_1 controls the spontaneous tendency of ants to explore a new environment; k_2 and m are parameters that depend on the time step (here fixed to 1 s).

Once an ant has entered a gallery i of the network, the time t_i required to travel the gallery is computed as follows:

$$t_i = \frac{d_i}{v}$$

with d_i the length of the gallery in centimeters and v the speed of the ant drawn from a normal distribution with mean v_{mean} and standard deviation v_{sd} .

At each symmetrical intersection, an ant has to choose between two branches a and b . The probability p_a for an ant to choose the branch a and p_b to choose the branch b at a symmetrical bifurcation are modeled as follows:

$$p_a = \frac{(k + C_a)^n}{(k + C_a)^n + (k + C_b)^n}$$

$$p_b = 1 - p_a$$

with k the intrinsic attractivity of branches a and b , C_a and C_b the quantity of pheromone on branches a and b , respectively, and n the degree of nonlinearity of the choice.

At an asymmetrical bifurcation, about 2/3 of the ants choose the branch deviating less from their original direction, whether the two branches are equally saturated by pheromone (as in our study) or unmarked (as in Gerbier et al. (2008)). We computed the probability p_a^* to select the

branch a and p_b^* to select the branch b at an asymmetrical bifurcation as follows:

$$p_a^* = p_a + p_{\text{pref}}$$

$$p_b^* = 1 - p_a^*$$

with

$$p_{\text{pref}} = l(-4p_a^2 + 4p_a)$$

l corresponds to the tendency of an ant to follow a path. It is positive if branch a deviates by a 30° angle from the ant's original direction and negative if it deviates by a 120° angle. When p_a is equal to 0.5 (i.e., $C_a = C_b$), then p_{pref} is equal to l . Because the two branches are equally marked by pheromone, the ant's choice is influenced only by the geometry of the bifurcation. Conversely, when one of the two branches becomes more marked with pheromone, then the ant's choice becomes influenced by the trail. Because this ant species is mainly guided by their pheromone trails, we assume that the influence of the bifurcation geometry progressively decreases as the difference in pheromone concentration between the two branches increases. Therefore, when P_a or P_b tend to 1 ($C_a \gg C_b$ or $C_a \ll C_b$), p_{pref} tends to 0.

Once the ant has crossed a bifurcation, it has a probability p_a to make a U-turn before reaching the end of the selected branch. This probability depends on the angle α (either 30° , 60° , or 120°) the ant has rotated to enter the branch.

An ant going to the food source deposits a quantity q of pheromone on the branch it comes from, just before reaching the bifurcation, and a quantity q on the branch it chooses, just after the bifurcation. An ant coming from the food source and going back to the nest deposits a quantity Q of pheromone at each of these points. As an approximation, we

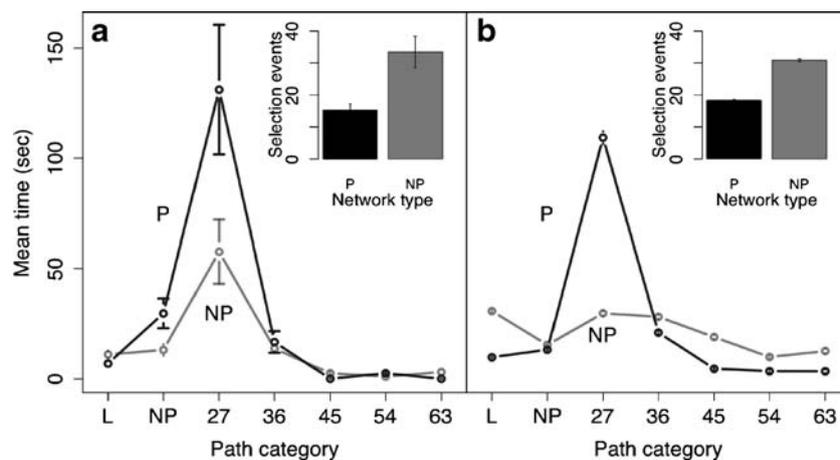


Fig. 3 Mean duration of selection events for each path category (main figures) and mean number of selection events (insets). **a** Experimental results ($n=10$). **b** Simulation results ($n=1,000$). Black curves and bars represent data for polarized networks. Gray curves and bars represent

data for non-polarized networks. Each point and bar represents the mean \pm standard error. Note that the standard errors for the simulation results are too small to be seen. L loop; NP no path

assumed that all ants in the model laid a trail (previous experiments by Deneubourg et al. (1990) have shown that the percentage of trail-laying ants is close to 90%). Since the average lifetime of the trail pheromone in *L. humile* is long (20–30 min, Deneubourg et al. (1990)) compared to the duration of the simulation (15 min), we neglected the evaporation of the pheromone in our model. One can also assume that the air in the galleries is rapidly saturated by the trail pheromone during an experiment. For this reason, we also considered that the diffusion of the trail pheromone in the network was negligible and thus did not implement a diffusion function in our model. We also ignored any possible effects of crowding, either in the galleries or at the food source. Finally, the time spent by an ant at the food source was modeled by a negative exponential law with a characteristic time τ as measured in Vittori et al. (2006).

The model was implemented in C++ and the simulations were run for 900 time steps of 1 s. One thousand simulations were run with the parameters given in Table 1. The parameters that had not been measured experimentally were estimated using the GENOUD (GENetic Optimization Using Derivatives) function provided by the RGENOUD package in R. This function combines evolutionary algorithm methods with a derivative-based (quasi-Newton) method to solve difficult optimization problems (for detailed explanations and evaluations about the GENOUD function, see Sekhon and Mebane (1998), Mebane and Sekhon (2001). The optimization was designed to minimize the difference between simulations and observations in the average number of ants in the network, and in the mean duration of selection events. Note that the optimization was applied only to the P-maze condition and not to the NP-maze one. Thus, free parameters were not optimized to

reproduce the differences observed in experiments between the two conditions. The genetic optimization was run five times for 200 generations in order to increase our confidence in the resulting parameters. In addition, we constrained the range of acceptable parameter values so that they remained biologically plausible. For example, values found for k and n were of the same order as those used in Goss et al. (1989).

Comparison of the model output with the experimental results

The simulation results were computed in the same manner as in the experiments. Note that, because of the 100-fold difference in sample size between the simulations and the experiments, we did not perform any statistical test to compare the results of the simulations to those of the experiments. The statistical power of such tests would be too low to be meaningful.

General network use

As in the experiments, the mean number of ants in the network followed a sigmoidal growth in both P-mazes and NP-mazes and the plateau reached in NP-mazes was greater than that reached in P-mazes (Fig. 2b). The mean number of used segments in simulations followed a qualitatively different dynamics than in experiments, reaching first a peak and then decreasing in simulations while reaching a plateau in experiments. But it displayed a difference between the two types of mazes similar to the one observed in the experiments, the mean number of used segments being higher in NP-mazes than in P-mazes in the second half of the simulations (Fig. 2b, inset).

Table 1 Parameters of the model

Parameter	Meaning	Value
k_0	Parameter that controls the maximal number of ants that can enter the network at each time step	0.003 ^c
k_1	Parameter that controls the spontaneous tendency of ants to explore a new environment	0.144 ^c
$k_2; m$	Parameters that control the speed of the recruitment at the nest	48 ^c ; 1.2 ^c
$v_{\text{mean}} \pm v_{\text{sd}}$	Mean and standard deviation of ant speed	1.1 ± 0.25 m s ^{-1b}
k	Intrinsic attractivity of bifurcation branches	60 ^c
n	Degree of nonlinearity of the pheromone attractivity	2.6 ^c
l	Tendency of an ant to follow the less deviating path	0.166 ^a
$p_{30^\circ}; p_{60^\circ}; p_{120^\circ}$	Probabilities to perform a U-turn after a rotation of 30°, 60°, or 120°	0.1 ^a ; 0.26 ^a ; 0.57 ^a
$q; Q$	Quantity of pheromone deposited by unfed (q) and fed (Q) ants	0.94 ^c ; 9.2 ^c
τ	Characteristic time spent by ants at the food source	179.9 s ^b

^a Parameters estimated experimentally

^b Parameters estimated experimentally in Vittori et al. (2006)

^c Parameters estimated by genetic optimization

Path selection

As in the experiments, a significant difference was found between P-mazes and NP-mazes for the mean number of selection events (18.4 ± 0.2 vs. 30.8 ± 0.5 , two-sample Wilcoxon test with continuity correction, $W=239,647.5$, $P<0.001$): once simulated ants had selected a path in P-mazes, they were less likely to switch to another path than simulated ants in NP-mazes (Fig. 3b, inset). A two-way ANOVA revealed a significant difference between the path categories ($F_{6,8461}=459.79$, $P<0.001$) and between the types of mazes ($F_{1,8461}=241.57$, $P<0.001$) for the mean duration of a selection event, and a significant interaction between these two factors ($F_{6,8461}=394.07$, $P<0.001$). In particular, when simulated ants in P-mazes selected a shorter path (one of the 27-cm paths), they used it for a significantly longer time than simulated ants in NP-mazes (Tukey HSD test, $P<0.001$; see Fig. 3b). These observations were similar to those obtained in the experiments.

Foraging efficiency

The foraging efficiency of the colony is difficult to evaluate in experiments because we would need to be able to distinguish between fed and unfed ants returning to the nest. We therefore used the model to evaluate the foraging efficiency in each type of maze. We defined the foraging efficiency as the ratio between the total number of fed ants returning to the nest over the total number of ants returned to the nest since the beginning of the virtual experiment. After only 900 s, the foraging efficiency in P-mazes was more than three times higher than in NP-mazes (0.318 ± 0.002 vs. 0.096 ± 0.001 , two-sample Wilcoxon test with continuity correction, $W=989,406$, $P<0.001$).

Discussion

Our results show that individual ants behave differently according to the geometry of the bifurcations they encounter during their foraging trips. In particular, workers of the Argentine ant show a clear preference when they encounter asymmetrical bifurcations: in our experiments, 66% of the ants chose the branch that deviated less from their original direction when the two branches were equally marked with pheromone. In addition, our results indicate that the individual probability of an ant to perform a U-turn increased with the turning effort the ant produced after crossing a bifurcation: the more its new walking direction diverged from its original direction, the more likely it was to perform a U-turn on the selected branch. Similar behavior has been found in *Lasius niger* ants: their

probability to perform a U-turn increases with the angle between their walking direction and the nest direction (Beckers et al. 1992; Dussutour et al. 2006).

At the collective level, our experiments revealed that Argentine ants were more dispersed and less capable of selecting a path in networks that did not present a geometrical polarization. Our model simulations confirmed that the differences between the individual behaviors of ants at symmetrical and asymmetrical bifurcations were sufficient to explain the discrepancies observed at the collective level between polarized and non-polarized networks. Additional sets of simulations (see Appendix) revealed that the improvement of the foraging efficiency and of the path selection ability in polarized networks was mainly due to the tendency of ants to follow the branch that deviated less from their original direction when reaching a bifurcation. In contrast, the higher probability to perform a U-turn on the branch that deviated more seemed to slightly favor the dispersion of ants inside the network.

In polarized networks, ants that went back to their nest and reached an asymmetrical bifurcation preferentially selected the branch that deviated less from their original direction. This branch was therefore more marked with pheromone and attracted more ants. Owing to the amplification of this individual tendency, the colony was more likely to select this branch. Because the less deviating branch at each bifurcation of the polarized network converged to the nest, ants had better opportunities to select one of the shortest paths than in non-polarized networks. As a consequence, the absence of polarization cues in non-polarized networks dramatically decreases food intake: after only 15 min, foraging efficiency estimated by simulations was three times lower than in polarized networks.

Amplification processes are widespread in group-living species and they are at the origin of some of the most impressive collective behaviors in social animals (see reviews in Camazine et al. (2001); Krause and Ruxton (2002); Couzin and Krause (2003); Detrain and Deneubourg (2006); Garnier et al. (2007)). They are based on a very simple principle: the more individuals perform a given behavior, the more likely other individuals will perform the same behavior. This explains why a slight difference in the tendency of individual animals to perform a given action is likely to propagate through the population resulting in the majority of individuals performing the same behavior. The amplification of behavioral differences via pheromonal recruitment in ants allows the ants to collectively choose one food source over another (Beckers et al. 1993; Sumpter and Beekman 2003; Dussutour et al. 2005) or to select a new nest site (Jeanson et al. 2004). Our study has shown that the amplification of behavioral biases significantly modifies the use and the functional efficiency of ant transport networks

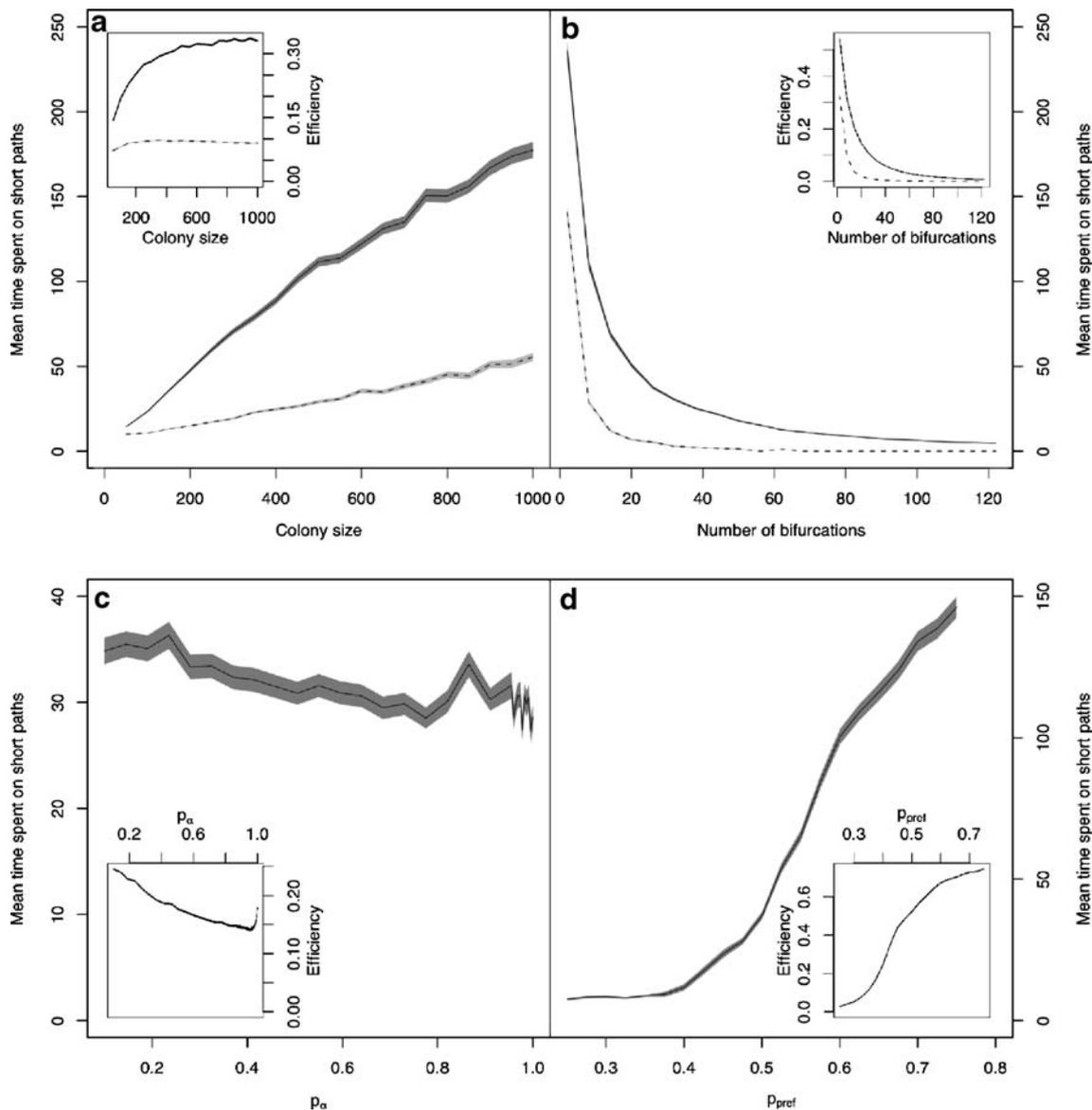


Fig. 4 Mean time spent on shorter paths (*main figure*) and mean foraging efficiency (*inset*) as a function of: **a** the size of the colony; **b** the number of bifurcations in the network; **c** the probability P_α to perform a U-turn on the most deviating branch after crossing a bifurcation; **d** the probability P_{pref} to select the less deviating path at a

bifurcation. Each curve represents the mean \pm standard error (*light and dark gray polygons*). In (a) and (b), *plain curves* represent data for polarized networks and *dashed curves* represent data for non-polarized networks

through an interaction between the networks' structure and the behavior of the ants.

How do ants form polarized networks? Recent experiments (data not shown) suggest that Argentine ants, like other ant species (Acosta et al. 1993; Jackson et al. 2004; Buhl et al. 2009), spontaneously form polarized networks during the exploration of their foraging environment. Several theoretical studies have investigated the formation of trail networks by different species of ants (see for instance Deneubourg et al. (1989); Edelstein-Keshet (1994); Edelstein-Keshet et al. (1995); Watmough and Edelstein-

Keshet (1995); Schweitzer et al. (1997)), but none of them specifically aimed at understanding the emergence of polarized bifurcations in such networks. To answer this question, it is necessary to investigate the individual behavior of an Argentine ant while it crosses a bifurcation and to characterize in detail the displacement of the ant just before the bifurcation, while it crosses it and just after it. We suspect that the polarization of the bifurcation results from a balance between the trail-following behavior of the ant, the inertia of its displacement, and the evaporation and the diffusion properties of the pheromone trail.

Conclusion

We conclude that biased individual behaviors coupled with amplification processes can have a major impact on the patterns of exploitation of transport networks in ants. Evaluating the efficiency of their transport networks on the basis of their structural properties may not fully reflect the actual performance of the colony. Understanding the coupling between ant behavior and network structure is therefore essential to accurately evaluate the efficiency of their nest galleries or their foraging trails.

In a more general context, our results emphasize the role of the behavior of network users in the functional efficiency of transport networks. This functional efficiency is the product of the structural properties of the network and of the network users' behaviors, and it should be evaluated as such.

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Appendix

Sensitivity analysis

We assessed the sensitivity of the model to the following parameters: the size of the colony, the number of bifurcations, the probability to perform a U-turn on the most deviating path (p_α) and the tendency to follow the less deviating path (p_{pref}). For each value of the tested parameter, we computed the time spent on shorter paths and the foraging efficiency after 900 s. One thousand simulations were run for each value of the parameters tested.

Size of the colony (Fig. 4a)

We varied the number of simulated ants from 50 to 1,000. We tested the simulated ants in both P-mazes and NP-mazes. The time spent on the shorter paths increased with the size of the colony in the two types of mazes. But it increased faster in P-mazes than in NP-mazes. The foraging efficiency remained low and relatively constant with the colony size in NP-mazes while it grew with the number of ants in P-mazes and eventually reached a plateau for large colonies. Note, however, that no crowding effect that could affect the collective behavior of the ants was implemented in the model.

Number of bifurcations (Fig. 4b)

We increased the number of bifurcations in the network by adding extra triplets of hexagons at the end of the network.

The total length of the network was kept constant and we tested simulated ants in P-mazes and NP-mazes. As the number of bifurcations increased, both the time spent on the shorter paths and the foraging efficiency dropped in P-mazes and NP-mazes. However, the decrease was slower in P-mazes than in NP-mazes.

Probability to perform a U-turn on the most deviating path (Fig. 4c)

We fixed l to zero (no tendency to follow the less deviating path) and varied p_{120° from 0.1 to 1 while p_{30° was kept equal to 0.1. The time spent on the shorter paths displayed only a small tendency to decrease as the probability to perform a U-turn on the most deviating branch increased while the efficiency of the colony decreased more clearly with increasing value of p_{120° . This effect was a consequence of the continuous pheromone laying of the ants. After crossing a bifurcation, the ant laid down a trail on the branch it had chosen. If it decided to perform a U-turn on this branch, it got over the trail it had just laid and therefore it reinforced it again. The choice of the next ant coming to the bifurcation was therefore slightly biased toward this branch. Because in this sensitivity analysis $p_{120^\circ} \geq p_{30^\circ}$, the most deviating branch was therefore more likely to be reinforced by ants performing a U-turn than the less deviating one. Counter intuitively, the higher probability to perform a U-turn on the most deviating branch favored the dispersion of the ants in the network. Note that the efficiency grew once p_{120° became close to one because in this case a low number of ants were able to reach the end of the most deviating branch (almost all of them performed a U-turn) and the only “escape way” was the less deviating branch.

Tendency to follow the less deviating path (Fig. 4d)

We fixed p_α to 0 (no U-turn) and we varied l from -0.25 (simulated ants preferentially selecting the most deviating branch) to 0.25 (simulated ants selecting the less deviating branch). As l increased, both the time spent on the shorter paths and the foraging efficiency increased. For large values of l , the foraging efficiency reached a plateau.

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