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FUNCTIONAL EFFICIENCY OF BIOLOGICAL TRANSPORT NETWORKS: WHY THE BEHAVIOUR OF NETWORK USERS MATTERS

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Abstract. We experimentally investigated the individual behaviour of the Argentine ant while crossing symmetrical and asymmetrical bifurcations in gallery networks. We showed that this ant behaved differently according to the direction it approached a network bifurcation. In the absence of any other orientation cue, ants crossing a symmetrical bifurcation equally selected both branching trails. On the contrary, 2/3 of the ants reaching an asymmetrical bifurcation chose the branch that deviates less from their coming direction. While foraging, ants lay down a pheromone trail that attracts other ants, which in turn reinforce the initial trail. This self-enhancing mechanism may eventually lead to the selection of the shortest route that connects the nest of the colony to a food source. We therefore studied with computer simulations the consequences of the preference expressed by ants at asymmetrical bifurcations on this collective path selection ability. We simulated colonies of ants foraging within a trail network, which bifurcations mimicked those found in natural trail networks (mostly symmetrical during foodbound trips and mostly asymmetrical during nestbound trips). Our simulation results clearly showed that the performance of the colony to find the shortest path linking the nest to a food source was better when simulated ants expressed the preference. Moreover after only fifteen minutes the foraging efficiency was three times higher when ants expressed the preference.

1 Introduction

Transport networks play a crucial role in the distribution of materials and information at all scales of the biological world. A lot of such networks have been studied so far, ranging from the internal 3D vascular systems of plants or animals [1-5] to the external 2D road networks built by human societies [6,7], or even to the shape of certain organisms such as slime mould [8,9] or fungi [10]. 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 architecture [11-15]. Outside the nest, some species of ants draw 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 [16].

Recent studies on transport networks in social insects have mostly focused on 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. [15] have shown that nests of *Cubitermes* termites display an excellent compromise between efficient connectivity within the nest and defence against attacking predators from outside the nest. In the ant *Messor sancta*, Bulh et al. [17] have shown that the gallery networks achieve a near optimal compromise between a highly efficient network and a highly robust one.

The structure of a network however does not necessarily reflect the way it is exploited by its users. Social factors for instance, as attraction toward or repulsion from conspecifics, or individual preferences may favour the use of certain parts of the network. As a consequence, topological and geometrical measurements do not always give a reliable picture of the functional efficiency of a given network.

In this contribution, we illustrate this statement through the example of foraging trail networks in ants. These trail networks form in general one or several dendritic trees originating from the nest of the colony [18]. In several ant species, field and experimental studies have shown that these trees display a particular structure: 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* [19]; *Monomorium pharaonis* [20]; *Formica aquilona* and *Linepithema humile*: data not published). Therefore an ant exiting the nest and moving toward 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 original direction of the ant. 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 (□30°) from the ant original direction than the other trail (□120°) that lead away from the nest. What could be the interest for ants to build foraging networks with such a geometrical particularity?

One part of the answer is related with the individual behaviour of ants. Jackson et al. [20] have demonstrated that when unfed pharaoh ants *M. pharaonis* going to a food source cross an asymmetrical bifurcation (that is more likely to occur in the journey back to the nest when they are fed) they have a high tendency to make a U-turn and come back to their point of departure. Fed ants do the same when they face a symmetrical bifurcation. Therefore *M. pharaonis* ants could use the geometry of the bifurcation as a network polarization cue to orient themselves correctly in the network.

Another part of the answer could rather be related to the collective behaviour of ants. While foraging, Argentine ants *L. humile* lay down a pheromone trail. This pheromone attracts other ants that follow the trail. Because these latter lay down additional pheromone, the trail attractiveness grows and the probability that more ants follow the trail increases. At a given bifurcation in a foraging network, this positive feedback may eventually lead most of the traffic to establish itself on one single branch if certain conditions of traffic and ant density are present [21]. Recent studies have shown that such collective decisions are strongly influenced by individual preferences that are amplified by the chemical recruitment process [22]. If the Argentine ant, like the pharaoh ant, expresses a preference when reaching an asymmetrical bifurcation, this should therefore affect its path selection ability and, as a result, the overall foraging efficiency of the colony.

In this paper, we investigate this hypothesis with laboratory experiments and computer simulations. We observe and quantify the individual behaviour of ants while they cross a symmetrical or an asymmetrical bifurcation inside a network of galleries. We will show that ants crossing an asymmetrical bifurcation express a preference for the branch that deviates less from their original direction and perform U-turns more frequently on the other branch. Based on these observations, we then build an individual-based model of the ants' displacements taking into account both this preference and the trail laying and following behaviour of this ant species. We eventually perform computer simulations of this model where simulated ants navigate between their nest and a food source through a complex network of galleries mimicking the geometry of natural networks. We perform simulations with and without the preference expressed by Argentine ants. We will show that colonies that express this preference display better performances to select the shortest path between the nest and the food source in the network and, as a consequence, increase their foraging efficiency. This will demonstrate the critical role of the individuals that operate within a transport network and their impact on its functional efficiency.

2 Biological experiments

2.1 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 as an invasive species with unicolonial habit (the species form a gigantic colony extending along the Mediterranean coast from Italy to Portugal and individuals mix freely among physically separated nests [23]). Ants were housed in artificial plaster nests (∅=10cm) without queen or brood and had access to an external foraging area. Twenty nests containing 2,000 workers each were used for this study. 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 [24] and with *Musca domestica* maggots. The colonies were starved for three days before each experiment.

2.2 Experimental procedure

The individual behaviour of the Argentine ant workers at bifurcations was tested in a series of alternatively inverted Y-mazes (see Figure 1). 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 and 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 (∅=20mm), each with a 15mm long and a 5mm wide access gallery, were carved. The depth of the galleries and chambers were 5mm. 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 tissue, which also ensured and indirect and diffuse lighting.

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. The angle between the three branches of the maze 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 one deviates by 120° from the access branch). Four situations were therefore 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 eating in order to offer the same type of bifurcation during the foodbound and the nestbound trips. Fifty ants were tested in each situation, which allowed us to observe one hundred unfed ants crossing a symmetrical bifurcation, one hundred unfed ants crossing an asymmetrical bifurcation, one hundred fed ants crossing a symmetrical bifurcation and one hundred fed ants crossing an asymmetrical bifurcation.

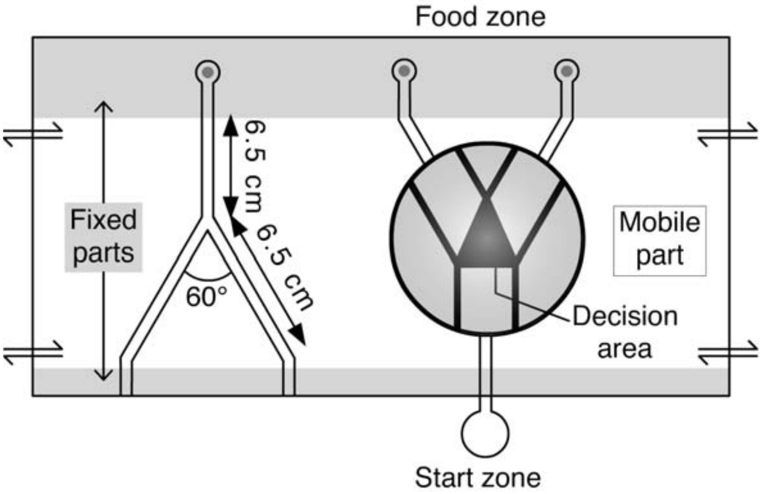

Figure 1: Schematic description of the experimental setup.

For each of the four tested situations, pieces of paper on which a fresh chemical trail had been deposited were placed before the tests at the bottom of the maze galleries. To avoid the effect of trail decay, the same pieces of paper were used during only 20 minutes. The trail pheromone duration of *L. humile* is indeed estimated to be close to 30 minutes [25]. 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 minutes by workers of another colony of the Argentine ant travelling between their nest and a food source (1 M solution of sucrose). This duration was sufficient to ensure that the paper was marked homogeneously. Since the Argentine ant is unicolonial [23,26] workers of one colony readily follow a trail laid by another colony.

A test started by collecting an ant in the foraging area of its colony. A small wood stick was introduced in the foraging area until an ant spontaneously climbed up and explored it. Then the wood stick and the ant were gently moved toward a small petri dish placed in front of an access gallery. During this short displacement (no more than 50cm) we took care of never touching the ant exploring the stick. To drop off the ant in the petri dish, one extremity of the stick was put in contact with the floor and we let the ant coming down spontaneously. Finally the ant explored the petri dish for at least one minute. All these precautions were taken to reduce disturbances 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, we recorded the initial choice of ants, that is 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 called “decision area” (see Figure 1). Note that in rare cases (8 cases over 400 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.

2.3 Experimental results

Independent of whether the ants crossed an asymmetrical bifurcation or a symmetrical one, there was no significant difference in the performance of fed and unfed ants (Fisher exact test: P=0.367 and P=0.396 respectively). We therefore pooled the data for foodbound and nestbound ants for the two types of bifurcations tested.

At the symmetrical bifurcation, ants choose equally between the two branches that followed the bifurcation (103 ants chose the right branch and 96 chose the left; binomial test: P=0.671). At the asymmetrical bifurcation, 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.

3 Virtual experiments

We investigated with computer simulations the impact of the ants’ preference to follow the branch that deviates less from their original walking direction.

3.1 Model

A colony of 500 simulated ants was given access to a network of galleries that mimicked the geometrical structure of natural dendritic networks (see Figure 2). The nest of the simulated colony was connected at one extremity of the network while a food source was connected at the opposite side alternatively at position A or B as indicated in Figure 2.

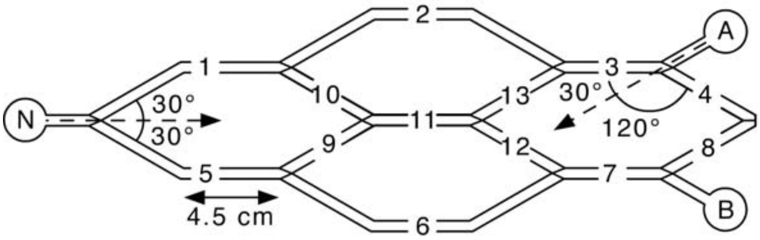

Figure 2: Schematic description of the simulated environment. N corresponds to the nest, A and B correspond to the possible position for the food source.

According to Camazine et al. [27] the flow of ants leaving the nest and entering the network at each time step (here fixed to one second) can be modelled as follows in the case of Argentine ants:

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

$C_{entrance}$ corresponds to the total quantity of pheromone deposited by 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 control the spontaneous tendency of ants to explore a new environment; k_2 and m regulates the speed of the recruitment at the nest.

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

At each symmetrical bifurcation 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 branche b at a symmetrical bifurcation are modelled 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 attractiveness 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 [28]). 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:

$$p_a^* = p_a + \alpha$$

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

with

$$\alpha = l(-4p_a^2 + 4p_a)$$

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 α is equal to l. Because the two branches are equally marked by pheromone, the ant choice is influenced only by the geometry of the bifurcation. Conversely when one of the two branches becomes more marked by pheromone, then the ant choice becomes influenced by the trail. Because this ant species is mainly guided by their pheromone trails [29], 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 tends to 1 ($C_a>>C_b$) or 0 ($C_a<<C_b$), α tends to 0.

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 considered that all ants in the simulations lay a trail whereas in experiments with *L. humile* the percentage of trail-laying ants is close to 90% [25]. Since the average lifetime of the trail pheromone in *L. humile* is long (20-30 minutes [25]) compared to the duration of the simulation (15 minutes), we neglected the evaporation of the pheromone in our simulations. No crowding effect, either in the galleries or at the food source, was considered in the simulations. Finally, the time spent by an ant at the food source was modelled by a decreasing exponential law with a characteristic time τ as measured in Vittori et al. [30].

3.2 Data analysis

For each second of the simulation, we computed the number of simulated ants present in each gallery of the network and we applied a moving average over a period of 30 seconds to reduce the noise introduced by the stochastic nature of our model.

For each second, we then specified the path selected by simulated ants as follows. Starting from the entrance gallery, we followed at each network bifurcation the gallery with the highest density of ants until we reached either a bifurcation followed by two empty galleries or a previously visited gallery or the food source. If we reached a bifurcation followed by two empty galleries, we defined the selected path as pertaining to the “no path” category. If we reached a previously visited bifurcation, we defined the selected path as pertaining to the “loop” category. There are 14 possible paths to reach the food source without using the same gallery twice. These paths can be classified in five categories according to their length: 27cm, 36cm, 45cm, 54 cm and 63cm. Thus we defined the path selected by the ants to reach the food source as pertaining to the category corresponding to its length. By repeating this process at each second of a simulation, we obtained the time sequence of path selection events. We eventually grouped all consecutive frames that showed the same path category into a single event that was called a selection event. This allowed us to compute over all the simulations:

- The mean number of selections events.
- The mean duration of a selection event for each selected path category.

We also evaluated the foraging efficiency of the simulated colony. We defined the foraging efficiency as the ratio between the total number of fed ants returned to the nest over the total number of ants returned to the nest since the beginning of the virtual experiment.

3.3 Simulation protocol

Parameter values are shown in **Erreur ! Source du renvoi introuvable.**. 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 (quasi-Newton) method to solve difficult optimization problems (for detailed explanations and evaluations about the GENOUD function, see Sekhon and Mebane [31] and Mebane and Sekhon [32]). The optimization was designed to minimize the difference between simulations and observations in the average number of ants in the network in one hand (data not shown), and in the mean duration of selection events in the other hand. The genetic optimization was run 5 times for 200 generations in order to increase our confidence in the resulting parameters. Besides, we constrained the range of acceptable parameter values so that they remain biologically plausible. For instance, values found for k and n were of the same order as those used in [33].

Parameter	Meaning	Value
k_0	Parameter that controls the maximal number of ants that can enter the network at each time step	$0.003^{\dagger}$
k_1	Parameter that controls the spontaneous tendency of ants to explore a new environment	$0.144^{\dagger}$
$k_2; m$	Parameters that control the speed of the recruitment at the nest	$48^{\dagger}$; $1.2^{\dagger}$
$v_{mean}\pm v_{sd}$	Mean and standard deviation of ant speed	$1.1\pm0.25\text{ms}^{-1**}$
k	Intrinsic attractiveness of bifurcation branches	$60^{\dagger}$
n	Degree of nonlinearity of the pheromone attractiveness	$2.6^{\dagger}$
l	Tendency of an ant to follow the less deviating path	0.166^{*}
$q; Q$	Quantity of pheromone deposited by unfed (q) and fed (Q) ants	$0.94^{\dagger}$; $9.2^{\dagger}$
τ	Characteristic time spent by ants at the food source	179.9sec^{**}

Table 1: Parameters of the model and their meaning. *: parameters estimated experimentally. **: parameters estimated experimentally in [30]. †: parameters estimated by genetic optimization.

We first tested our model in two different situations. In the first situation, simulated ants that crossed an asymmetrical bifurcation expressed a preference for the branch that deviated less from their original direction. This situation corresponded to what was observed during the experiments and the value of l was set as in **Erreur ! Source du renvoi introuvable.**. In the second situation, we removed the preference and therefore we set l to 0. For each situation we run thousand simulations for 900 time steps of 1 second (15 minutes).

We also perform a more systematic exploration of the impact of l value on the collective behaviour of the simulated colony. To that purpose we varied l value between -0.25 (simulated ants preferentially selected the most deviating branch) to 0.25 (simulated ants preferentially selected the les deviating branch).

3.4 Simulation results

1. Path selection

A significant difference was found between simulations with and without the preference for the mean number of selection events (18.4±0.2 versus 30.8±0.5, see inset in Figure 3 (a), two samples Wilcoxon test with continuity correction, W=239647.5, P<0.001): once simulated ants expressing the preference had selected a path they are less likely to switch to another path than simulated ants that did expressed the preference. A two-way ANOVA revealed a significant difference between the path categories (F=357.67, df=6, P<0.001) and between the types of ants (expressing or not the preference, F=413.46, df=1, P<0.001) for the mean duration of a selection event, and a significant interaction between these two factors (F=362.3, df=4, P<0.001, see Figure 3 (a)). In particular when simulated ants expressing the preference selected a shorter path (one of the 27cm paths), they used it for a significantly longer time than simulated ants that did not expressed the preference (Tukey HSD test, P<0.001).

2. Foraging efficiency

After only 900 seconds, the foraging efficiency of simulated colonies expressing the preference was more than three times higher than the foraging efficiency of colonies that did not express the preference (0.626±0.003 versus 0.196±0.002, see Figure 3 (b), two sample Wilcoxon test with continuity correction, W=989406, P<0.001).

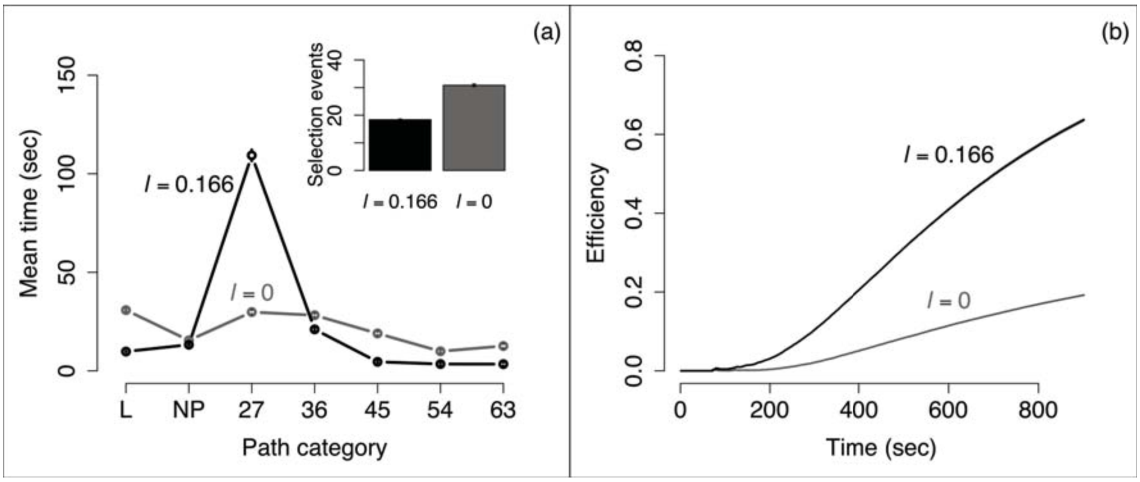

Figure 3: (a) Mean duration of selection events for each path category (main figures) and mean number of selection events (insets). (b) Mean foraging efficiency as a function of the time. (a) and (b) Black curve and bar represent data for l=0.166 (ants express a preference for the branch that deviates less from their original walking direction). Grey curve and bar represent data for l=0 (ants have no preference). Each point and bar represents the mean±standard error (n=1000). L=loop; NP=no path.

3. Sensitivity analysis

As shown in Figure 4, both the time spent on the shorter paths and the foraging efficiency increase with the tendency l of an ant to follow the branch that deviates less from its original direction. For large value of l the foraging efficiency reaches a plateau. Interestingly, the performance of the simulated ants that expressed a preference equal to the one measured in experiment is very closed to this plateau.

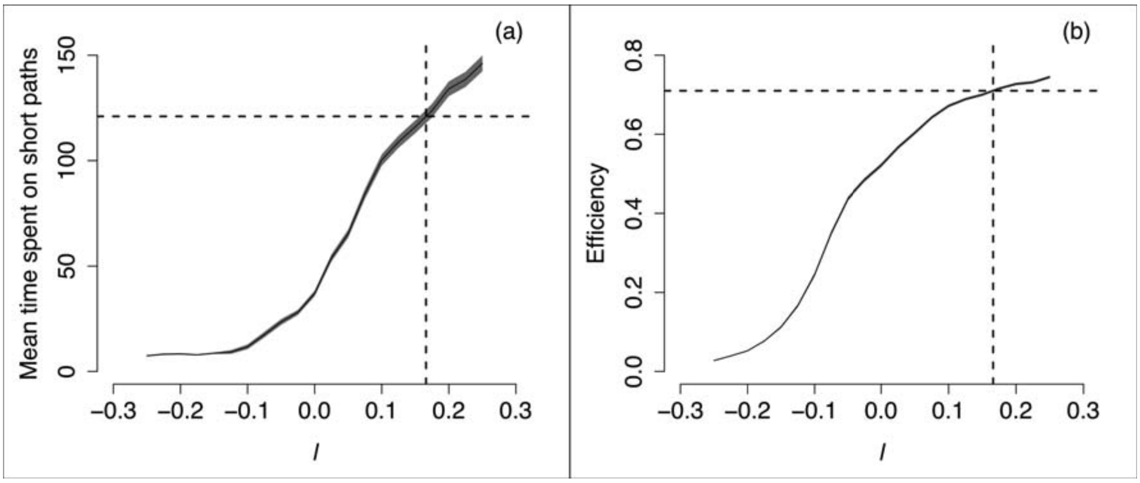

Figure 4: Mean time spent on shorter paths (a) and mean foraging efficiency (b) as a function of the tendency *l* of an ant to select the branch that deviates less from its original direction. Each curve represents the mean±standard error (n=1000). The crossing between the dashed lines represents the value obtained with *l*=0.166, as measured in experiments with Argentine ants. Interestingly, the model predicts that the preference expressed by Argentine ants leads to a performance after 15 minutes closed to the maximal performance.

4 Discussion

Our results show that workers of the Argentine ant do make biased choice when crossing an asymmetrical bifurcation: 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.

At the collective level, our model simulations predicted that this preference for the less deviating branch should have major consequence on the ability of the colony to select one of the shorter paths in the network. Indeed, simulated 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 preference, the colony was more likely to select this branch. Because the less deviating branch at each bifurcation of the network converged to the nest, ants had better opportunities to select one of the shorter paths than simulated ants that did not express the preference. As a consequence, the absence of preference for the less deviating path dramatically decreased the food income: after only fifteen minutes, the foraging efficiency estimated in simulations was three times lower in colonies that did not express the preference than in colonies that did express it.

Amplification processes are widespread in group-living species and they are at the origin of some of the most impressive collective behaviours in social animals (see reviews in [27,34-37]). They are based on a very simple principle: the more individuals perform a given behaviour, the more likely other individuals will perform the same behaviour. This explains why a slight difference in the tendency of individual animals to perform a given action is likely to propagate in the population so that soon the majority of individuals perform the same behaviour. The amplification of behavioural preferences by chemical recruitment in ants is responsible for instance of several biased collective decisions during foraging [22,38] or the selection of a new nest [39].

As illustrated by our work, the existence of behavioural biases and their amplification can significantly modify the use and the functional efficiency of ant' transport networks. This latter results indeed from the interaction between the networks' structure on one hand and the behaviour of the ants on the other hand. Evaluating the efficiency of ants' transport networks only on the basis of their structural properties may not fully reflect the actual performance of the colony. Understanding the coupling between ant behaviours and network structure is therefore essential to accurately estimate the efficiency of their nest galleries or their foraging trails.

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