

Commentary

Ant traffic rules

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Summary

Many animals take part in flow-like collective movements. In most species, however, the flow is unidirectional. Ants are one of the rare group of organisms in which flow-like movements are predominantly bidirectional. This adds to the difficulty of the task of maintaining a smooth, efficient movement. Yet, ants seem to fare well at this task. Do they really? And if so, how do such simple organisms succeed in maintaining a smooth traffic flow, when even humans experience trouble with this task? How does traffic in ants compare with that in human pedestrians or vehicles? The experimental study of ant traffic is only a few years old but it has already provided interesting insights into traffic organization and regulation in animals, showing in particular that an ant colony as a whole can be considered as a typical self-organized adaptive system. In this review we will show that the study of ant traffic can not only uncover basic principles of behavioral ecology and evolution in social insects but also provide new insights into the study of traffic systems in general.

Key words: ants, traffic, foraging, trail, self-organization.

Introduction

Looking closely at the spectacle of ants walking hectically back and forth on their foraging trails, gently following, overtaking and passing each other, one cannot help but think, in a surge of anthropomorphism, of the confusion that sometimes occurs in our crowded pedestrian streets or of the nightmarish traffic-jams that obstruct the roads circling our big cities. This spectacle has always been a source of amazement for naturalists. In the fourth century BC Aristotle wrote in his *History of Animals* “*They [ants] come back to their nest by following a rather straight line and on the path they do not hinder one another*”. Do ants really fare better than us when it comes to traffic management? Is their traffic always as fluid and organized as it seems? Are they able to avoid traffic-jams and to regulate their density on their trails? Do they act cooperatively when they move on their trails? Do they actively maneuver to avoid bumping into each other or is every ant going for itself, without paying attention to its nestmates? Was Plutarch right when he wrote in the first century AD “*Those that are unladen move aside from the path to give way to those that are laden*”? Are there really priority rules between ants that depend on their size, direction of movement and on whether or not they carry a load? Can the organization of traffic increase in some ways foraging efficiency? These questions and others have been addressed in recent research whose findings will be reviewed in this commentary paper.

Origin and characteristics of foraging trails in ants

Collective movements, involving, sometimes, several thousands of individuals, are observed in a lot of organisms, ranging from bacteria to vertebrates (reviewed by Couzin, 2009). In most animals, however, these movements are unidirectional because they are linked to migratory phenomena and thus involve individuals moving in the same direction from one part of their foraging range

to the other. Along with humans (Moussaid et al., 2009) and some species of social caterpillars (Fitzgerald, 1996), social insects are one of the rare group of animals in which collective movements are predominantly bidirectional. Social insects are central-place foragers, which means that they retrieve food to their nest at the end of each foraging trip. When exploiting abundant food sources, a lot of species lay chemical trails along which individuals commute, moving back and forth between their nest and the food sources [ants (Hölldobler and Wilson, 1990), termites (Miura and Matsumoto, 1998a), stingless bees (Jarau, 2009)]. In some species of ants the flow of individuals on these trails can be extremely high, reaching more than hundred ants per minute [red wood ants (Holt, 1955), leaf cutting ants (Wirth et al., 2003), army ants (Gotwald, 1995)]. Bidirectional traffic is also observed in ants on the trails that link the different nests of polycolony colonies (Hölldobler and Wilson, 1990).

The trail pheromone of ants originates from different glands (Billen and Morgan, 1998) and is a multicomponent signal acting both as a recruitment and an orientation signal (Hölldobler, 1995). Chemical mass recruitment by trail pheromone is a self-organized process based on positive (trail reinforcement by recruited individuals) and negative (pheromone evaporation, food depletion) feed-backs. It allows ants to regulate their flow according to the type, quantity and quality of the food being exploited, as well as to make collective decisions such as choosing the resource to be exploited or the path along which to establish their trail to reach a food source (reviewed by Detrain et al., 2008). In some species of ants exploiting long-lasting food sources, such as seed-harvesting ants or leaf-cutting ants, the initial chemical trail can turn into a physical trail called a trunk-trail that can persist for days or weeks and that can be followed on the ground even in the absence of traffic (Anderson and McShea, 2001). Physical trails are costly to build

and maintain since they are actively cleared of vegetation and obstacles by ants (Howard, 2001). They offer a smooth surface to the ants, which facilitates load transport and increases the rate of locomotion (Holt, 1955). In some species they can be progressively buried into the ground or covered by galleries to offer protection from predators or adverse weather conditions (Kenne and Dejean, 1999).

Basic traffic theory and what they imply for ant traffic

The problem faced by ants in managing their traffic on foraging trails is the same as that faced by road engineers: since trails are costly to build and maintain for the colony, they should be used optimally (Burd et al., 2002). Optimality is ensured if ants are able to maintain their flow close to the capacity of the trail, i.e. the maximum value of the flow allowed by its width (Fig. 1). This corresponds ultimately to maximizing the rate of food delivery to the nest (Burd et al., 2002; Burd, 2006). If ants behave optimally they should adjust the width of their trails so that this capacity is close to the maximum flow of forager arrival allowed into the nest, which in the end is constrained by the diameter of the nest entrances. If the intensity of traffic accommodated by the trail is too high, food caches, consisting of an accumulation of resource material, are sometimes created in front of the nest entrances (Hart and Ratnieks, 2000). Since the flow is calculated as the product of ant speed and density, there is an optimal value for the density of ants on the trail to achieve maximum capacity (Fig. 1); the flow decreases below this value because of the decrease of ant density, and it decreases in the same way above this value because of the decrease of ant speed due to a high rate of time-consuming head-on collisions (Burd and Aranwela, 2003; Dussutour et al., 2005b). Ants could reduce this rate and maintain the same flow by enlarging their trails. However, this has several costs for the colony. First, it has a cost of manufacture, especially when foraging trails continue inside underground galleries as is the case for some leaf-cutting ant species. Besides, the presence of large physical obstacles along ant trails often impedes their enlargement. Second, it has a cost for the orientation of the ants. In fact, since trail pheromone is as much a recruitment as an orientation signal, enlarging the trail will do no good because it will decrease the density of pheromone spots deposited on the substrate and thus increase the risk of ants losing their way. Finally, it has a cost a cost in terms of foraging efficiency because it will reduce the rate of physical contacts between ants which are known to play an important role in information transfer and ultimately on the foraging efficiency of the colony (see below).

Spatial and temporal traffic organization on ant foraging trails

The rate of collisions at high density can be reduced, and the capacity of the trail increased, if there is some kind of traffic organization on the trails. As in vehicle traffic, traffic organization in ants can take two different forms: the traffic can be organized either on a spatial or on a temporal basis.

A spatial organization of traffic is observed when some degree of lane segregation occurs, i.e. when the flows of inbound and outbound ants are not completely intermingled. Of course, the amount of lane segregation observed on ant trails is never as high as on our highways. However, it is sufficient to reduce the rate of head-on collisions between ants and thus to increase the capacity of their trails. A clear lane segregation is observed in the raiding columns of the species of the army ant *Eciton burchelli*: inbound laden ants occupy the central part of the column whereas outbound ones move on both of its flanks (Couzin and Franks, 2002)

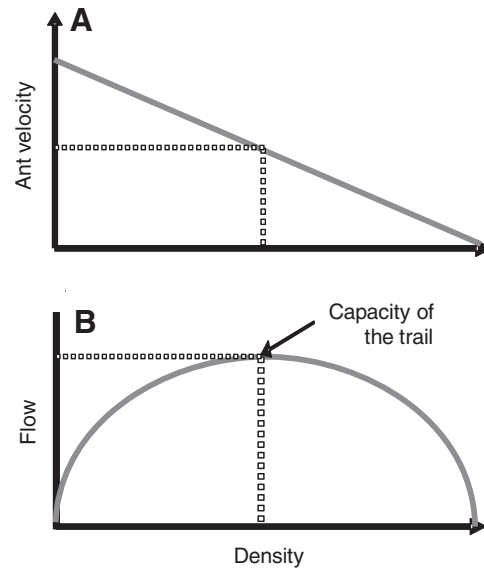


Fig. 1. Fundamental diagrams of traffic theory showing (A) the relationship between the speed and the density of moving particles and (B) the relationship between the flow and the density of moving particles.

(Fig. 2A). An individual-based model shows that this three-lane structure is generated by an asymmetry of turning rates during the avoidance maneuvers between outbound and inbound ants: inbound ants deviate less from their initial direction than outbound ants. The model further shows that this organization allows the maintenance of the flow of ants on the trail close to its capacity. Interestingly, a similar organization is observed on the foraging columns of the open-air foraging Nasute termites of the genera *Hospitalitermes* (Miura and Matsumoto, 1998a), *Longipeditermes* and *Lacessititermes* (Miura and Mastsumoto, 1998b): returning workers travel in the central lane of the column and are flanked on both sides by a lane of outgoing workers. Moreover, in these termites as in the army ant *Dorylus nigricans* (Gotwald, 1995), the foraging column is protected on both sides by a caste of specialized workers called soldiers that stand still, perpendicularly, at some distance from the column and that possess particular morphological structures (large mandibles for army ant soldiers and a gland containing noxious liquid in the cephalic capsule for Nasute soldiers) to defend themselves against predators.

Why a three-lane and not a two-lane organization as on our highways? Such an organization would indeed decrease the probability of head-on encounters and thus increase traffic flow. As noted by Couzin and Franks (Couzin and Franks, 2002), however, a two-lane organization would probably be less stable than a three-lane one. In fact, any asymmetry in the frequency or intensity of trail pheromone deposition between inbound and outbound workers would lead ants from the lane where the pheromone is less concentrated to drift towards the lane where the pheromone is more concentrated, which will force ants traveling on this lane to move further aside and thus lead to a progressive shift in the trail position. Such an asymmetry in trail pheromone deposition has been reported in several species of ants [*Lasius niger* (Mailleux et al., 2005), *Monomorium pharaonis* (Jackson and Chaline, 2007)]. Moreover, the three-lane organization observed makes sense from a functional point of view as it protects the most valuable workers of the colony, i.e. the workers loaded with food. Since they are flanked on both sides by a lane of outbound workers, these workers have less risk

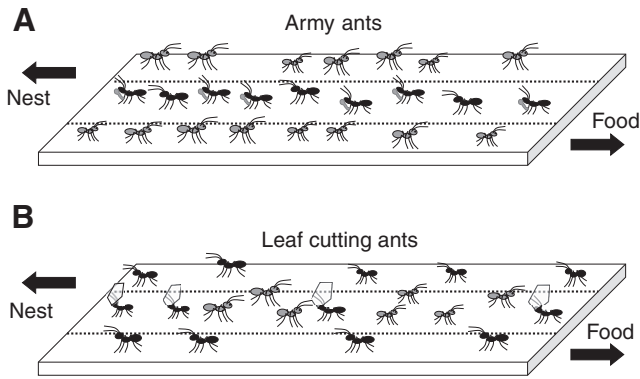


Fig. 2. Schematic drawings showing the spatial organization of traffic in (A) the army ant *Eciton burchelli* (B) the leaf-cutting ant *Atta colombica*.

of straying from the foraging column and they are also protected from predation or food robbing.

Some degree of lane segregation has also been observed by Dussutour (Dussutour, 2004) in the leaf-cutting ant *Atta colombica* when traveling in the laboratory on a 50 mm-wide bridge installed between their nest and a box containing leaf material (Fig. 2B). Of the 15% inbound ants that returned to the nest with a leaf fragment, 94% traveled on the central part of the bridge. Unladen inbound ants on the other hand tended to travel mostly on both sides of the bridge. As for outbound ants, 67% of them traveled on the central part of the bridge and, irrespective of their size, they gave way to inbound laden ants in 80% of the head-on encounters. The same priority rule has been observed by Burd et al. (Burd et al., 2002) in another leaf-cutting ant, the species *Atta cephalotes*, and by Holt (Holt, 1955) in the red wood ant *Formica rufa*. As in army ants this behavior can probably be explained by the fact that laden returning ants are less mobile and have less maneuverability than unladen outbound ants (Zollikofer, 1994); they are thus slower and have more difficulties in deviating from their initial direction.

A. colombica is a highly polymorphic species and, using the same 50 mm-wide bridge, Dussutour (Dussutour, 2004) observed that the location of the workers on the bridge also depended on their size. Independent of their travel direction, *minor* workers (<2.5 mm in length) walk mostly on the central part of the bridge. Because of their size these workers generally do not deviate or deviate just a little from their initial direction after making a frontal encounter. *Minor* workers may also be less sensitive to the trail pheromone and they may keep to the central part of the trail where the density of pheromone spots is probably higher (Kleineidam et al., 2007). *Submedia* (2.5–4.0 mm) and *media* (4.0–5.5 mm) workers, by contrast, walk mostly on the central part of the bridge in their outbound trip and they are given way to by unladen returning ants of the same size. When returning unladen to their nest, however, they walk mostly on both sides of the bridge and they give way to outbound ants. This asymmetry in priority rules as a function of travel direction could be explained by the fact that outbound ants could be more motivated than inbound unladen ants to reach the end of the trail or, alternatively, by the fact that outbound ants rely more heavily on the pheromone trail than inbound ants and thus avoid straying from the foraging column. *Major* workers (5.5–7.0 mm) walk equally on the central part or on both sides of the bridge in their outbound trip but show a clear preference for walking on the bridge margins in their inbound trip. Irrespective of

their travel direction, they have equal probability of giving way to or being given way by other unladen workers.

The spatial organization of traffic observed in *A. colombica* is much less strict than that observed in the army ant *E. burchelli*, as the outbound and inbound flows of ants are partly intermingled. There may be several explanations to account for this difference. First, this could be explained by the fact that army ant workers are totally or almost totally blind (Gotwald, 1995) and thus almost entirely rely on the chemical trail to orient on their foraging columns. Leaf-cutting ant workers, by contrast, are equipped with compound eyes and can therefore partly rely on visual cues (light, terrestrial landmarks) to orient on foraging trails (Ribeiro et al., 2009). It could therefore be more risky for inbound army ants than for inbound leaf-cutting ant workers to stray from their column. Second, the difference could be due to the slower speed of leaf cutting ants. Independent of temperature, army ants do indeed move much faster than leaf cutting ants. They should thus have a higher inertia and experience more difficulties in deviating from their initial direction. Third, the partial lane segregation observed in *A. colombica* could be due to the fact that the speed difference between unladen and laden workers may be higher in leaf-cutting ants than in army ants. On a wide path, where the probability of making costly head-on collisions with ants coming from the opposite direction is low, leaf-cutting ant workers returning unladen to the nest may thus benefit from overtaking their laden nestmates by traveling on the sides of the foraging column. Finally, a last hypothesis to account for the weak degree of lane segregation observed in leaf-cutting ants could be the importance of physical contacts in these ants: the high rate of head-on collisions observed on the foraging trails of *A. colombica* may promote information transfer and stimulate outbound workers to cut and collect leaf material at the end of the trail, thus contributing to increased foraging efficiency (see below).

While moving on their foraging area ants sometimes face physical constraints that limit the width of their trails and result in bottlenecks. This occurs for example in arboreal ants when they travel on small branches or lianas, or in litter ants when they walk on fallen branches or when they use structural guidelines such as natural cracks, furrows or walls to establish their trails (Dussutour et al., 2005a). Ants may also face bottlenecks at the entrance of their nest or, once inside their nest, within the network of subterranean galleries leading to the chambers where they stock food. In order to avoid traffic-jams that could decrease the rate of food return to the nest, workers of the black garden ant *Lasius niger* organize their flow on a temporal basis with alternating clusters of inbound and outbound ants crossing narrow passageways (Dussutour et al., 2005b). This organization limits the rate of time-consuming head-on collisions and thus allows ants to maintain the same travel duration as that observed on wider paths. As a consequence, a narrow path can sustain the same flow intensity as a wide path, which saves ants from engaging in the costly work of enlarging their trail to avoid a decrease of the rate of food return to their nest. Close examination of the behavior of individual ants shows that outbound and inbound clusters of ants arise at the level of the bottlenecks and are generated by priority rules. Ants arriving at a bottleneck give way to the ants coming from the narrow part of the trail, leading to an accumulation of ants at the level of the constriction. When the path is free, the waiting ants cross the narrow section of the trail. This occurs in all cases except when an ant is closely following another ant that has just entered the narrow part of the trail, in which case it enters the narrow section of the trail, whether or not another ant is coming from the opposite

direction. This latter rule can be considered as a low-form of cooperation since the leading ant frees the path for the ants behind her. Such oscillatory changes in flow direction are also observed in bi-directional streams of pedestrians going through narrow passages (Helbing et al., 2005). An individual-based model shows that in ants the formation and size of the clusters are governed by the interplay between the value of the flow intensity and the priority rules. At flow intensities comparable to that observed in the experiments (approximately one ant per second), the distribution of the size of the clusters obtained in the simulations is close to that observed experimentally (Fig. 3). At lower flow intensities, however, the distribution of the size of the clusters is similar to that obtained with a random sequence of inbound and outbound ants. Finally, above a certain value of the flow intensity a phase transition is observed and the mean size of the clusters increases abruptly (Fig. 3, inset). The model also shows that the temporal organization of the flow arises only when the cooperative rule described above in which the leading ant of each group frees the path for the ants that are behind, is implemented in the model.

A temporal organization of traffic is also observed in the leaf-cutting ant *Atta colombica* when workers are forced to move on narrow paths, allowing the passage of one or two individuals at a time (Dussutour et al., 2009a). There are, however, several important differences between *A. colombica* and *L. niger* that makes the rules governing the temporal organization in the former species a bit different. First, in *A. colombica*, in contrast to *L. niger*, workers vary greatly in size and the bigger workers of *A. colombica* move much more rapidly than the smaller ones (Dussutour, 2004). Second, leaf-cutting ant workers carry their load externally, not internally as those of *L. niger*. Leaf-cutting ant workers carry leaf fragments in their mandibles and they are thus much bulkier than unladen outbound workers. Therefore, whereas in *L. niger* there are no significant differences in locomotory rate between nestbound laden ants and outbound emptied ants (Dussutour et al., 2005b), in leaf-cutting ants, by contrast, laden individuals generally progress more slowly than unladen ones. And third, in leaf-cutting ants, unlike mass recruiting ants, which feed on liquid, not all returning ants carry a load. The reason for this is still unclear. In *A. colombica*, Howard (Howard, 2001) clearly demonstrated that about 5% of the forager force do not transport load because it is engaged in trail clearing, and in *Atta* spp. *minim* workers seem to have an important role in the maintenance of the pheromone trail (Evison et al., 2008). In leaf-cutting ants therefore the flow of inbound workers is more heterogeneous than in

L. niger. In *A. colombica* it is essentially the differences in size and locomotory rate that form the basis of the priority rules that generate oscillations in flow direction. Because laden returning ants have less maneuverability than unladen outbound ants on narrow paths, they are given way to by the latter (Fig. 4A). Unladen returning ants, however, give way to outbound ants (Fig. 4B). Moreover, unladen returning ants do not attempt to overtake the laden ants in front of them. Since they move faster than laden ants, unladen ants are forced to decrease their speed and to adjust it to the laden ants in front of them (Fig. 4A), much as a small car following a heavy truck will do. This decrease is compensated for by the fact that, by staying in a cluster instead of moving in isolation, inbound unladen ants limit the number of head-on encounters with outbound ants. A quantitative analysis shows that the delay induced by these head-on encounters would actually be twice as high as the delay induced by the forced decrease in speed incurred by ants staying in a cluster (Dussutour et al., 2009a). Outbound ants move to the side of the narrow path, allow the passage of the cluster of incoming ants, and return to the centre of the path (Fig. 4A). This behavior prevents the fission of incoming groups of ants. In addition, as outbound ants moving to the side are frequently followed by other ants, this produces an alternation of inbound and outbound groups of ants following each other closely, thus generating the temporal organization of traffic.

One of the indirect consequences of the temporal organization observed in *A. colombica* traveling on narrow paths is that it increases the rate of contacts between emptied outbound workers and returning laden workers. In fact, since returning unladen ants adjust their speed to the laden ants in front of them, most clusters of returning ants are headed by a laden ant (Dussutour et al., 2009a). As a consequence, outbound ants make head-on contacts mostly with laden ants, not with unladen ants. These contacts are generally brief but they can sometimes lead to the transfer of leaf fragments between workers and generate the formation of multistage transport called 'bucket brigades' (Anderson et al., 2002). They have been hypothesized to increase information transfer on food availability and to stimulate outbound workers to cut and transport leaf fragments (Roces and Bollazzi, 2009; Farji-Brener et al., 2010) (but see Burd, 2000). This phenomenon may explain why foraging efficiency, i.e. the load returned per forager, is greater on narrow paths than on wide paths (Dussutour et al., 2007) or on paths where head-on contacts are promoted between outbound and inbound laden workers, e.g. by the presence of a height constraint on the path hindering the progression of the ants transporting upright leaf fragments (Dussutour et al.,

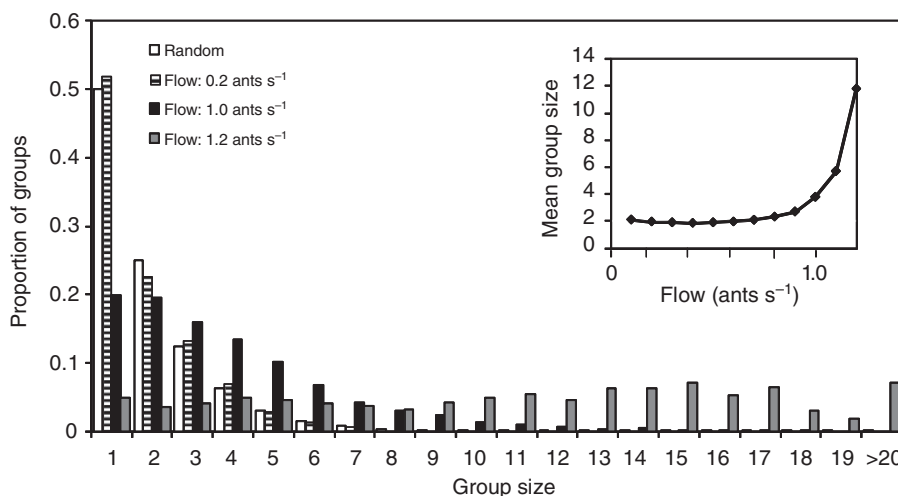


Fig. 3. Results of simulations showing the distribution frequency of the size of inbound and outbound groups of workers of the ant species *Lasius niger* crossing a 90 mm long, narrow passageway as a function of the intensity of the flow at the entrance of the passage. The inset shows the value of the mean group size for increasing value of the flow.

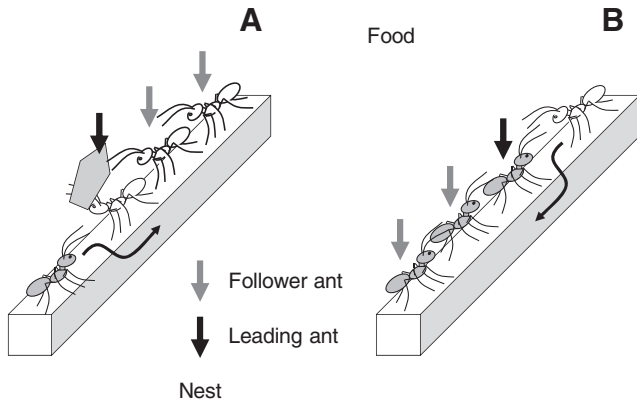


Fig. 4. Priority rules generating oscillations in flow direction in the leaf cutting ant *Atta colombica* moving on narrow paths. (A) Outbound ants give way to inbound laden ants; (B) inbound unladen ants give way to outbound ants.

2009b). Interestingly, if a higher rate of contacts with laden nestmates leads to a higher probability of leaf cutting, one could also think that a lower rate of contacts could lead to a lower probability of leaf cutting. These responses could thus allow ants to rapidly track the availability of resources at the end of a trail, without the need of traveling its whole length. Depending on the change in the rate of contacts with laden returning ants, outbound ants could decide to make a U-turn to the nest, to shift to another trail at a bifurcation, or to leave the trail altogether in order to search for new resources in the environment. Another consequence of this finding is that a wide foraging trail not only could be more costly in terms of building and maintenance, but could also result in a lower foraging efficiency. Therefore, given a certain intensity of the flow of ants on a trail, there should be an optimal width of that trail for which the rate of contacts between outbound and laden returning ants is such that foraging efficiency is maximized. Following our earlier line of reasoning, one can conclude that if ants behave as road engineers they should adjust the width of their trails so as to maximize, not the flow of ants *per se*, but rather the foraging efficiency (Burd et al., 2002): a trail too wide could lead to a lower rate of food return to the nest by decreasing foraging efficiency, whereas a trail too narrow would have the same effect by decreasing the ant locomotory rate.

Traffic regulation by route selection in ants

Another way one can avoid overcrowding and jamming on a narrow path is by selecting one or more alternative paths. This could seem to be an easy task but it is not, for humans and ants alike. In fact, in both cases the cohesive forces between individuals are generally much stronger than the dispersive forces. Pedestrians or car drivers are reluctant to venture in the unknown and they often prefer to follow their fellows, even at the risk of crowding or being stuck in traffic jams. Mass recruiting ants on the other hand, rely essentially on trail pheromone when traveling between their nest and a food source. When given the choice between several paths, they will thus always select the path with the highest pheromone concentration; even a tiny difference in pheromone concentration between two paths leads to the selection of only one path (Beckers et al., 1992; Sumpter and Beekman, 2003). In the Argentine ant *Linepithema humile*, once a trail has been established, foraging workers stuck to it, even if a shorter alternative path becomes available (Goss et al., 1989).

Dussutour et al. (Dussutour et al., 2004) have shown that, when faced with two narrow paths of equal length reaching the same food

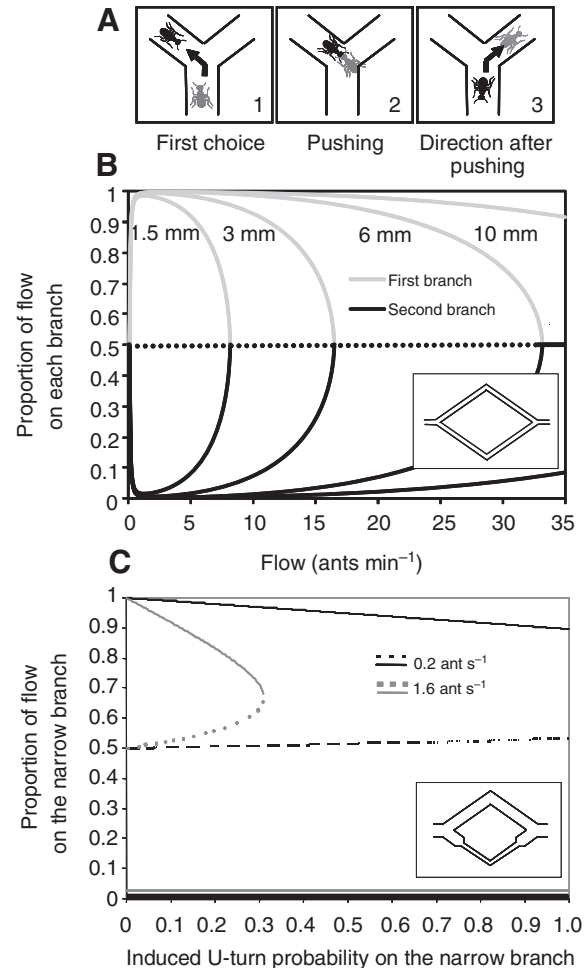


Fig. 5. (A) Schematic drawing showing the inhibitory interactions observed at path bifurcations between workers of the ant *Lasius niger*. (B) Simulation results showing that when ants have the choice between two narrow paths of equal length leading to the same food source, inhibitory interactions at the bifurcations lead to a symmetrical traffic above a critical value of the flow intensity, which is an increasing function of the branch width. The traffic is asymmetrical below the critical values. The curves correspond to branches of 1.5, 3, 6 and 10 mm width. (C) Simulation results showing that inhibitory interactions are responsible for the choice of the wide path when ants are given the choice between two paths of equal length but different widths (3 vs 10 mm). For a flow intensity comparable to that observed in the experiments (1.6 ants s⁻¹), the system permits two stable solutions (asymmetrical traffic: the traffic concentrates either on the wide or on the narrow path) and one unstable solution (no choice: symmetrical traffic) below a critical value of the probability of inhibitory interactions. The system allows only one stable solution (the choice of the wide path) above this critical value. For a low flow intensity (0.2 ants s⁻¹) the system allows two stable solutions (the choice of the narrow or the wide path) and one unstable solution (no choice: symmetrical traffic), whatever the value of the probability of inhibitory interactions. In B and C the inset shows the experimental set-up. The dashed lines represent the unstable solutions and the continuous lines the stable ones.

source, workers of the species *Lasius niger* avoid being slowed down in traffic-jams by dividing their flow equally between the two paths. This phenomenon occurs very rapidly at the beginning of the recruitment process, before the traffic volume would begin to be affected by overcrowding. A mathematical model shows that it is based on inhibitory interactions between workers: if a worker

reaching a bifurcation between the two paths makes a head-on collision with a worker coming from the opposite direction on one path, it is pushed to the other path (Fig. 5A). In the absence of pushing, the traffic remains asymmetrical, independently of the traffic volume. When pushing occurs at the same rate as in the experiment, the traffic is asymmetrical for low traffic volumes but becomes symmetrical for critical values of the flow intensity that are an increasing function of the path width (Fig. 5B). The same type of inhibitory interactions is also responsible for the choice of the less overcrowded wider path when ants are given the choice between two paths of equal lengths but different widths (3 mm versus 10 mm; Fig. 5C) (Dussutour et al., 2006). On the one hand, for low traffic volume the system permits one unstable (symmetrical traffic) and two stable (asymmetrical traffic: the flow of ants is concentrated either on the wide or on the narrow path) solutions, whatever the value of the probability of inhibitory interactions. On the other hand, for the same volume of traffic as that observed in the experiments (1.6 ants s^{-1}), the system permits only one solution (the traffic is concentrated on the wide path) when the probability of inhibitory interactions is high (≥ 0.3). Monte-Carlo simulations show in addition that the wide path is still chosen when it is more than three times longer than the narrow path. This occurs because the reduction in travel time due to a shorter distance traveled on the narrow path is rapidly offset by the delay incurred by the high rate of head-on collisions due to overcrowding on the narrow path (Dussutour et al., 2006). In all these examples, traffic regulation ultimately allows ants to maintain a high rate of food return to the nest, an essential asset in the context of food competition occurring in natural environments.

Conclusion and perspectives

In recent years research on ant traffic organization has provided new insights for the study of traffic in pedestrians (Nishinari et al., 2006) and vehicles (Peters et al., 2006). Of course, ants do not move like pedestrians or vehicles and there are some important differences to consider when comparing their traffic organization. In the first place, ants moving on a foraging trail are from the same colony. They thus share a common objective and work to increase the overall fitness of the group, which is generally not the case for pedestrians or car drivers. Ants should, therefore, be expected to act more cooperatively than pedestrians or car drivers. And in fact, this is what they do: whereas the traffic of pedestrians or vehicles is essentially ruled by external constraints (enforced rules), inhibitory interactions (avoidance) and negative feed-backs (slowing-down, jamming), in ants positive interactions (contacts allowing the exchange of information) and positive feed-backs (trail following and reinforcement) seem to be as essential as inhibitory interactions to allow a smooth and efficient traffic. Second, and most importantly, ants do not have the same mechanical constraints as pedestrians or vehicles: because of their small mass they have a low inertia and therefore are not damaged by collisions. This allows a certain degree of mixing of opposite flows on foraging trails which ends up, as explained above, to be beneficial for the colony. Nevertheless, even at the scale of organisms such as ants, the inertia of movement and maneuverability is different between small and large ants: small ants waste less time than large ants in collisions. One could therefore speculate that traffic organization could obey some allometric rules. For example, the degree of lane segregation could be higher in species of ants characterized by big workers than in those characterized by small workers. Given the huge difference in worker size observed in the ant species recruiting by trail

pheromone (for example, a *Paraponera clavata* worker is about 20 times bigger than a *Wassmannia auropunctata* worker), this could be easily tested.

The examples reviewed in this paper show that ants are able to solve complex problems of traffic regulation by using simple rules that are not imposed externally and arbitrarily (as in vehicle traffic) but that result from local direct (contacts) or indirect (trail pheromone) interactions between individuals. The solutions emerge from these interactions and the ant colony as a whole thus behaves as a self-organized biological adaptive system (Camazine et al., 2001). This explains why in recent years ant traffic has become a source of inspiration for scientists working with large groups of massively interacting particles in disciplines as diverse as molecular biology (Tabony, 2006), statistical physics (Chowdhury et al., 2004) and telecommunication sciences (Blum, 2005). The study of ant traffic could certainly benefit from more interactions with these disciplines, not only from a theoretical but also from a technical point of view, for example in the development of innovative multiple-target automatic tracking techniques. Traffic-like movements in different organisms do share common properties and one can assume that increased scientific exchanges between biological and physical disciplines in the future could potentially lead to the emergence of a new coherent framework of traffic-like movements in science.

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