

RESEARCH ARTICLE

Bi-directional movement characteristics of *Camponotus japonicus* ants during nest relocation

Qiao Wang^{1,2}, Weiguo Song^{1,*}, Jun Zhang¹ and Siuming Lo²

ABSTRACT

Foraging and nest relocation forming a bi-directional traffic of outbound and inbound individuals in one-lane organization are two main activities in an ant's life. In this paper, we conducted an experiment on nest relocation of loaded and unloaded ants, moving back and forth between the old nest and the new one. In the experiment, we observed both uni- and bi-directional traffic flow. The headway–speed relationships indicate that the ants showed the same sensitivity to the distance headway in the two types of flow. For bi-directional traffic flow, head-on encounters and giving-way behavior between ants moving in opposing directions were a common occurrence. It took one unloaded ant 2.61 s to solve a head-on encounter with another unloaded ant. Compared with unloaded ants, loaded ants had a lower moving speed, but were less likely to be impacted by a head-on encounter. In the observation region, both sudden stop and head-on encounters contained two phases: deceleration and acceleration. Our analysis indicates that the relaxation time in the deceleration process is less than that in the acceleration process. The reduction of movement efficiency of encountering two discontinuous ants is larger than that when encountering two successive ants (0.18). This is owing to the absence of head-on encounters with following ants. The bi-directional traffic of ants under experimental conditions investigated in this study may inform future studies of high-efficiency movement in collective behavior and traffic systems.

KEY WORDS: Collective behavior, Bi-directional ant traffic, Head-on encounter, Movement efficiency

INTRODUCTION

An ant colony, containing a few dozen to millions of individuals (Oldroyd, 1968), consists of one or more fertile females called queens, fertile males, workers and soldiers (Oster and Wilson, 1978). Ants show a strong division of labor; for example, workers are responsible for establishing buildings, enlarging their nest, collecting food and larvae. All ants residing in one colony are regarded as a unified entity and support their colony by collectively working (Flannery, 2011). Thus, collective motion is the main pattern in an ant's life (Hölldobler and Wilson, 1990). In recent years, the collective behavior of ants under emergency conditions has been widely studied (Dias et al., 2013; Haghani and Sarvi, 2017; Wang et al., 2015). Experimental evidence for a 'faster is slower'

effect comes from an evacuation experiment of ants under stressed conditions (Soria et al., 2012), but jamming and clogging were not observed near the exit (Boari et al., 2013).

In the wild, bi-directional traffic of inbound and outbound individuals is formed in ants' foraging activities (Gravish et al., 2015; John et al., 2004), which differs from that of most animals, whose movements are uni-directional. The formation of a foraging trail benefits from the pheromone that ants deposit it on the ground. This pheromone can attract subsequent ants to follow the trail and ultimately find the food resource, and the final destination of this trip is their nest (Norman and Hughes, 2016; Wilson, 1990). Before workers carry food to the nest, cleared physical trails are built, which can facilitate load transport and increase the rate of foraging efficiency (Bruce et al., 2017). Certainly, it takes time and energy for workers to build and maintain physical trails (Bochynek et al., 2017; Howard, 2001). Thus, wider trails could take workers more time and energy, which decreases foraging efficiency.

As in vehicle traffic, some degree of lane segregation in ant traffic spatial organization is observed, i.e. the trails of inbound and outbound ants are not intermingled completely. This is good for reducing the rate of head-on encounters. In some ant traffic, three-lane trails are common, such as in the army ant *Eciton burchelli* (Couzin and Franks, 2003). Compared with the two-lane organization, three-lane traffic would probably increase flow because there would be fewer head-on encounters (Fourcassié et al., 2010). Moreover, the three-lane organization is useful from a functional point of view as it can protect the loaded ants from being robbed. However, because of width limitation of their trails, such as for arboreal ants traveling on small branches or lianas, or litter ants walking on fallen branches or using structural guidelines (natural cracks, furrows or walls), one-lane organization also occurs in ant trails (Dussutour et al., 2005a). Taking *Atta colombica* as an example, the inbound and outbound trails show a weak degree of lane separation (Dussutour, 2004). One hypothesis for explaining the intermingled trail is that the high rate of head-on encounters observed in forging trails of *A. colombica* is beneficial for information exchange and helps outbound workers to find food easily. Furthermore, it is not necessary to take more time and energy to build and enlarge the trail and clear the obstacles in it. Additionally, narrow paths can maintain the pheromone in a high concentration, which can select following ants strongly for foraging. In this way, it contributes to improving foraging efficiency. Alternatively, in one-lane bi-directional traffic, the outbound ants make head-on encounters with loaded ants but not with unloaded inbound ants. These head-on encounters result in the transfer of food between workers and this multistage transport is called 'bucket brigades' (Anderson et al., 2002; Lee and Kim, 2017). This suggests that the foraging efficiency is greater with a narrow path than with a wide path (Dussutour et al., 2007).

One-lane organization in ant traffic is common. The associated foraging or nest relocation efficiency is higher than that with wide

¹State Key Laboratory of Fire Science, University of Science and Technology of China, Hefei 230027, China. ²Department of Architectural and Civil Engineering, City University of Hong Kong, Hong Kong 999077, China.

*Author for correspondence (wgsong@ustc.edu.cn)

 W.S., 0000-0001-5390-6787

paths in which lane segregation occurs. In bi-directional ant traffic, head-on encounters, as the main pattern for ants moving in opposite directions, play an important role in foraging and nest relocation efficiency. In previous studies (Couzin and Franks, 2003; Dussutour et al., 2004; Schultheiss et al., 2015), the researchers were interested in qualitative analysis of the spatial organization of trails. In this paper, the main goal was to study the bi-directional flow of ants (*Camponotus japonicus*) in a narrow path quantitatively. We conducted nest relocation experiments and ants were stimulated to emigrate from their nest by changing the environmental conditions (illumination and humidity) and supplying food.

MATERIALS AND METHODS

Insects

Nest relocation experiments were performed on *Camponotus japonicus* Mayr 1866, a species of black ant native to East Asia, to investigate the collective behavior of ants; 427 worker ants from one colony (without a queen) were collected in Shaanxi Province of China and transported to the laboratory. They were placed in a plaster box with a plastic lid and the wall of the box was painted with Fluon to prevent the ants from escaping. The box was kept at room temperature ($24 \pm 2^\circ\text{C}$) under natural light/dark cycles with sufficient water and honey provided. When the experiment started, the ants had been raised in the laboratory for 3 months and the average length of their bodies was 1.03 ± 0.11 cm (mean \pm s.d.).

Experimental setup

Fig. 1A shows the arena for the experiments. Two polypropylene boxes of the same size (41 cm long \times 29 cm wide \times 23 cm high), with walls coated with Fluon, were used as the new and the old nests. A transparent plastic pipe (100 cm long and 0.8 cm in diameter) connected the two nests from the bottom corners; its width allowed two ants to move side by side. The old nest had no food or water in it and it was placed in a well-lit environment, whereas the new nest was in a comfortable environment (dark and damp surroundings)

with an adequate supply of food (honey) and water. Thus, the ants were easily persuaded to move from the old nest to the new one. A digital video camera with a frame rate of 25 frames s^{-1} placed over the pipe was used to record the experiment. A 20 cm-long area located at the middle of the pipe was selected as the observation region (see Fig. 1B). When the experiment began, we put the whole colony including dead ants into the old nest.

Statistical analysis

We extracted trajectories of ants from the video sequences manually by tracking the ant's head. From the 2D trajectories we first define the free speed $v_f(i)$ of the i th ant using the following equation:

$$v_f(i) = \frac{L}{T}, \quad (1)$$

where $L=20$ cm denotes the length of the observation region, and T is time spent by an ant moving in the observation region. The free speed can reflect the motion characteristics of ants in the channel when there is no disturbance (homodromous or opposite-moving ants). In order to investigate the speed variation in more detail, we calculated the instantaneous speed $v_i(t)$ of ants as:

$$v_i(t) = \frac{x_i(t + \Delta t/2) - x_i(t - \Delta t/2)}{\Delta t}, \quad (2)$$

where $x_i(t)$ represents the coordinate of ant i in the x direction at time t and Δt is 0.32 s in this study. Instantaneous speed can be used to investigate the interaction among ants in the observation region.

RESULTS

Time, speed and distance headway in ant traffic

The old nest was in a poor environment, whereas the new nest was suitable for ants to live in. The strong contrast made ants relocate from their old nest to the new one spontaneously. When the ants were introduced into the old nest, they became active and displayed irregular movements within the box. Those near the entrance to the

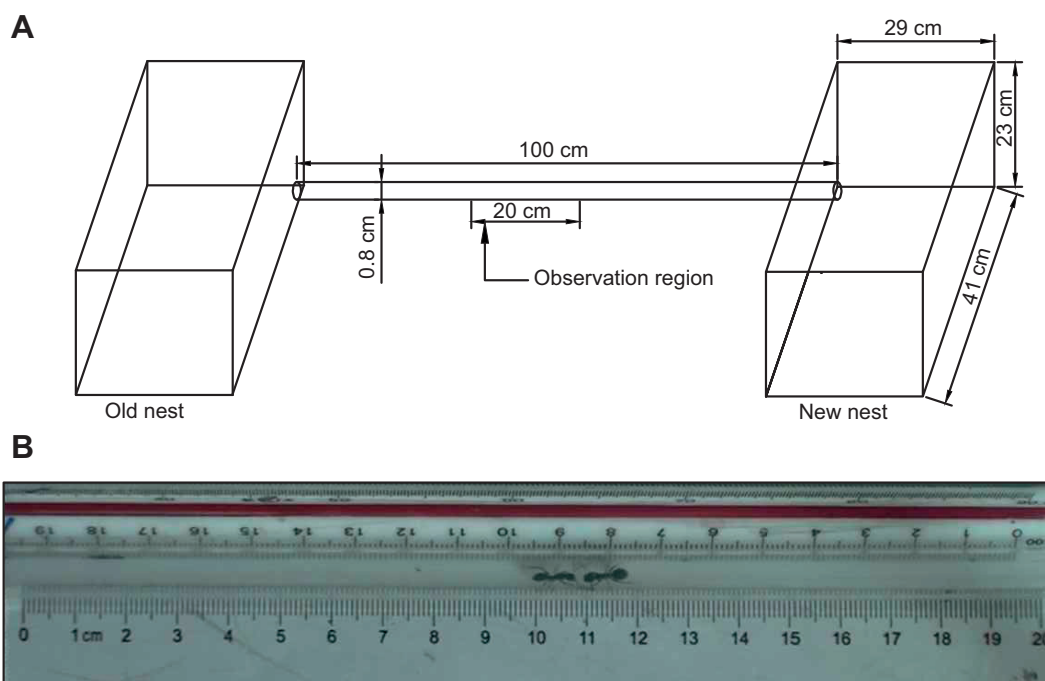


Fig. 1. Schematic diagram of the experimental setup. (A) Two boxes of the same size were connected by a transparent pipe, with an observation region of 20 cm in the middle part of this pipe. (B) A photograph showing that outbound and inbound ants made head-on encounters in the observation region.

pipe spent less time finding it and arrived at the new nest through this pipe. The first ant entered the observation region 2.23 min after the experiment began. As time elapsed, most ants in the old nest were attracted by pheromones deposited by the pioneer ants and eventually found the new nest as shown in Fig. 2. In order to exchange information with ants in the old nest, ants in the new nest returned to the old one. Thus, outbound and inbound ants encountered each other at some point within the pipe. After a period of time, a stable concentration of pheromone was formed, so that workers began to carry the dead bodies of ants to the new nest through the pipe. The first of these 'loaded' ants (see below) appeared in the observation region at 64.28 min. No inbound loaded ant was observed.

Because of the division of labor, some ants are just responsible for exploring trails whilst carrying nothing, i.e. they are unloaded ants. In contrast, the main job for others (the loaded ants) is carrying dead bodies from the old nest to the new one in this nest relocation experiment. In the observation region, the free speed of unloaded ants was $2.87 \pm 0.76 \text{ cm s}^{-1}$ while that for loaded ants was $2.22 \pm 0.43 \text{ cm s}^{-1}$, as displayed in Fig. 3. There was a significant difference in the average free speed of loaded and unloaded ants (t -test: $T=8.32$, $P<0.05$).

In the process of nest relocation, two interactions were observed among ants: following behavior for homodromous ants (uni-directional traffic) and head-on encounters with ants moving in the opposite direction (bi-directional traffic). Experiments with pedestrians (Cao et al., 2016; Jelić et al., 2012) revealed that speed is dependent on distance headway with several linear relationships. Here, we also investigated the relationship between distance headway and speed. Here, distance headway is defined as the available distance between neighboring ants, i.e. the distance between the head of the following ant and the tail of the preceding one in uni-directional traffic and the distance between the heads of two opposite-moving ants in bi-directional traffic. In uni-directional ant traffic, several ants moving in the same direction passed through the observation region, and the relationship between distance headway and speed is plotted in Fig. 4A. Similarly, the distance headway in bi-directional traffic also affects the speed of ants, as shown in Fig. 4B. However, according to the fitted curve, there are two linear regimes (a strongly constrained regime and a free regime)

with different slopes for uni-directional traffic and three linear regimes (a strongly constrained regime, a weakly constrained regime and a free regime) for bi-directional traffic. Comparison of the slope and intercept for uni-directional and bi-directional traffic flow shows that they have the same slopes (0.095, 0.094), while the intercept (0.306) of uni-directional traffic is larger than that of bi-directional traffic (0.0723). In the free regime, the average values of speed were 3.0 and 2.85 cm s^{-1} for uni-directional and bi-directional traffic, respectively.

Head-on encounters

Trajectories

At 9.73 min, the first inbound ant entered the observation region. Gradually, more and more inbound ants moved in the pipe, which induced more head-on encounters between outbound and inbound ants in the observation region (see Fig. 2). Their trajectories were displayed in Fig. 5. When the ants moving in opposite directions encountered each other, they gave way by shifting to the left or the right side. The trajectories clearly present a wavy form, and a remarkable detour emerged when the ants gave way to those from the opposite direction.

Deceleration and acceleration

Fig. 6A,C,E,G depicts the temporal–spatial diagram of ant movement in the observation region for one outbound unloaded ant encountering another, inbound unloaded ant, two inbound discontinuous unloaded ants (decreasing speed twice), two inbound successive unloaded ants (just decreasing speed once) and one inbound loaded ant, respectively. Correspondingly, the evolution of speed with position in the observation region is shown in Fig. 6B,D,F,H. In this experiment, we observed that when two unloaded ants encountered each other, their antennae were in contact for a period of time. We hypothesize that the purpose of antennae contact is information exchange. As can be seen from Fig. 6, the head-on encounter of unloaded ants resulted in a decrease of their speed. After opposite-moving ants separated completely, unloaded ants restored their speed rapidly. Fig. 6B,D,F shows that the head-on encounter process consists of three phases: deceleration due to the encounter, stop for information exchange and then acceleration to free speed. In the deceleration phase, unloaded ants

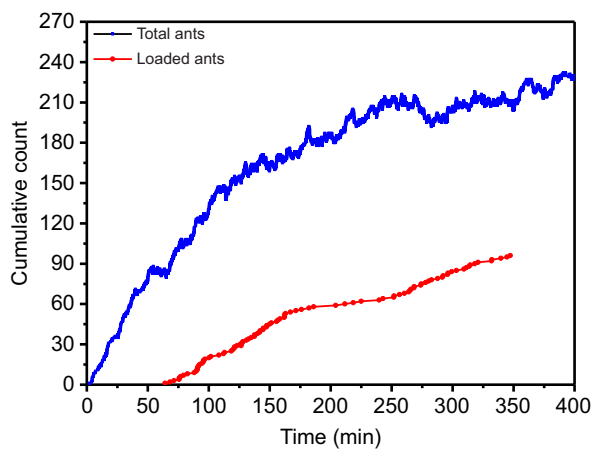


Fig. 2. Cumulative count of ants moving from the old nest to the new nest. The blue curve records the total ants in the nest relocation experiment, in which outbound and inbound ants are included. The red line shows the outbound ants which carried dead bodies (loaded ants).

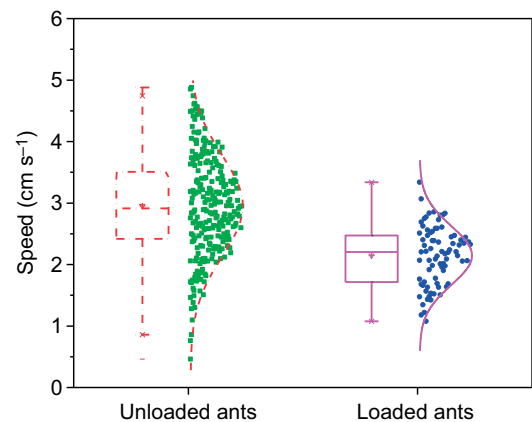


Fig. 3. Distribution of ant speed. Box plots show the average speed of unloaded (red) and loaded ants (magenta), and the green and blue dots represent the free speed of single unloaded and loaded ants. The red dashed line and magenta line indicate the distribution of free speed for unloaded and loaded ants.

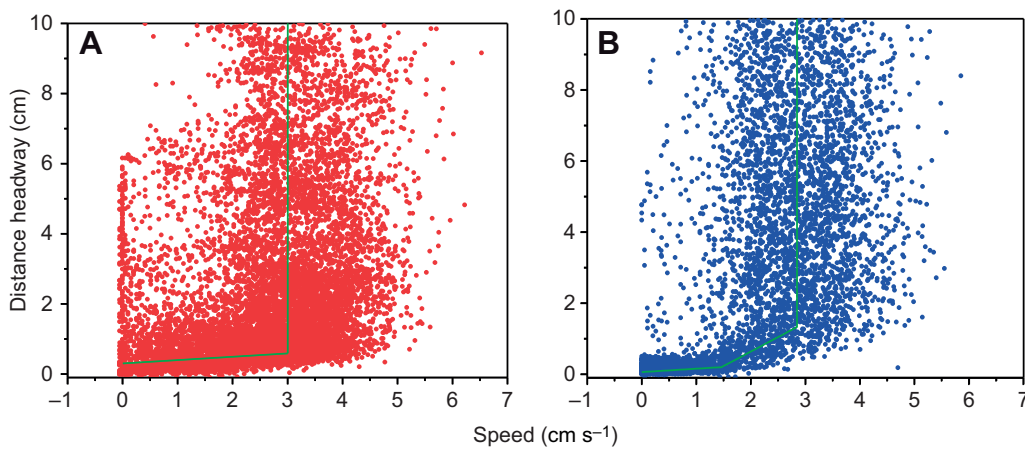


Fig. 4. Scatter diagrams and linear curve fitting (green line) of the distance headway–speed relationship for ant traffic. (A) Uni-directional traffic; (B) bi-directional traffic. The single dots represent the instantaneous speed of ants for the corresponding distance headway. In the constrained regime, the linear curve is according to the peak values of distance headway for each bin ($\Delta v=0.1$, where v is speed).

decrease their speed from free speed to zero. Correspondingly, during the acceleration phase, the ants regain their speed. In addition, the time spent in the deceleration phase is less than that in the acceleration phase. In this work, we tracked 49 loaded ants, involving 23 encounters with other ants. As shown in Fig. 6G, H, the speed of the outbound loaded ant did not decrease significantly, unlike that of unloaded ants when they make head-on encounters with others. Thus, head-on encounters have less effect on the motion of loaded ants. This may be because loaded ants have a higher mass; therefore, head-on encounters may have less effect on the speed of loaded ants due to inertia. Furthermore, loaded ants utilize their two strong jaws, which are attached to the head below the antennae, when they carry dead bodies (Borror et al., 1989); thus, dead bodies of large size may affect the function of the antennae to some degree. Additionally, the presence of a dead body meant that the process of antennae contact, i.e. information exchange, was not observed clearly. Furthermore, without external interference, loaded ants did not stop suddenly.

As shown in Fig. 6, deceleration and acceleration are the basic phases for ant encounters. In terms of behavior following head-on encounters with opposite-moving ants, we calculated their movement characteristics, such as the evolution of speed with time in the deceleration and acceleration phases, by averaging these two phases. In the deceleration phase, time zero is the time at which

all the recorded ants moved with free speed, and the time at which the speed of ants reduced to zero was the same. For the acceleration phase, speed was zero at zero time but increased for all subsequent time steps. Fig. 7A shows the deceleration and acceleration phases for head-on encounters and the exponential curves. The deceleration and acceleration curves conform to exponential distribution. The exponential function is expressed as:

$$v = v_f + A \times \exp(-t/\tau). \quad (3)$$

Using the same analysis method as Ma et al. (2010) and Moussaïd et al. (2009), τ in Eqn 3 is defined as the relaxation time that an ant needs to decelerate to minimum speed in the deceleration phase and accelerate to free speed in the acceleration phase. A larger τ indicates that ants require more time to complete the deceleration and acceleration phases. The mean relaxation time for the deceleration phase was 0.16 s, which is smaller than that for the acceleration phase (0.6 s).

In the observation region, some ants stopped suddenly without any external interference and then started moving again. Fig. 7B shows the deceleration and acceleration phases for these sudden stops. The results show that $\tau=0.17$ s for the deceleration phase and $\tau=0.42$ s for the acceleration phase. Comparison of the head-on encounter process and sudden stops shows the mean relaxation time of the deceleration phase is similar, but ants took less time to restore their speed from zero in the sudden stop condition.

Reduction of movement efficiency

In the foraging performance of ants, head-on encounters between workers are common in ant traffic. Head-on encounters reduced motion speed, thus diminishing movement efficiency (Burd and Aranwela, 2003). In this work, the reduction of movement efficiency caused by head-on encounters was studied quantitatively. The head-on encounter process was defined as the time elapsed from the contacting of antennae of two opposite-moving ants to the complete separation of them. When an unloaded ant encountered an ant moving in the opposite direction, the average walking duration in the observation region was 2.61 ± 1.13 s. When it encountered two successive ants, the walking duration in the observation region was 4.24 ± 1.52 s. From this result, it can be seen that encountering two successive ants head-on would cause a smaller increase in walking duration and therefore result in a higher movement efficiency (improvement of 18.9%) compared with encountering two discontinuous ants. As observed, encounters with other ants reduced movement efficiency by a reduction of speed to enable

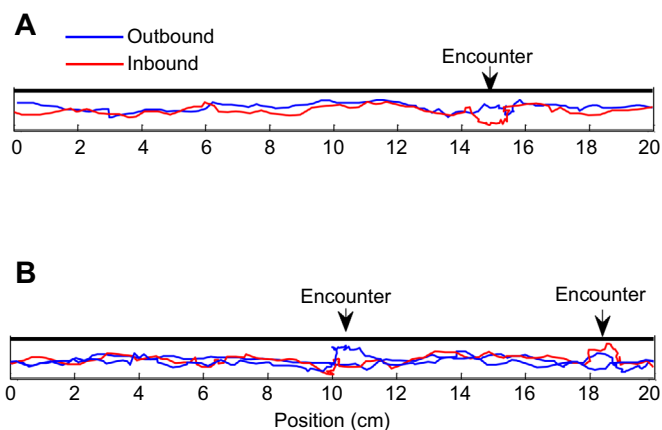


Fig. 5. Trajectories of ants encountering each other from opposite directions. (A) An outbound and an inbound ant from opposite directions encountering each other in the observation region. (B) Two outbound ants and one inbound ant encountering each other at different positions.

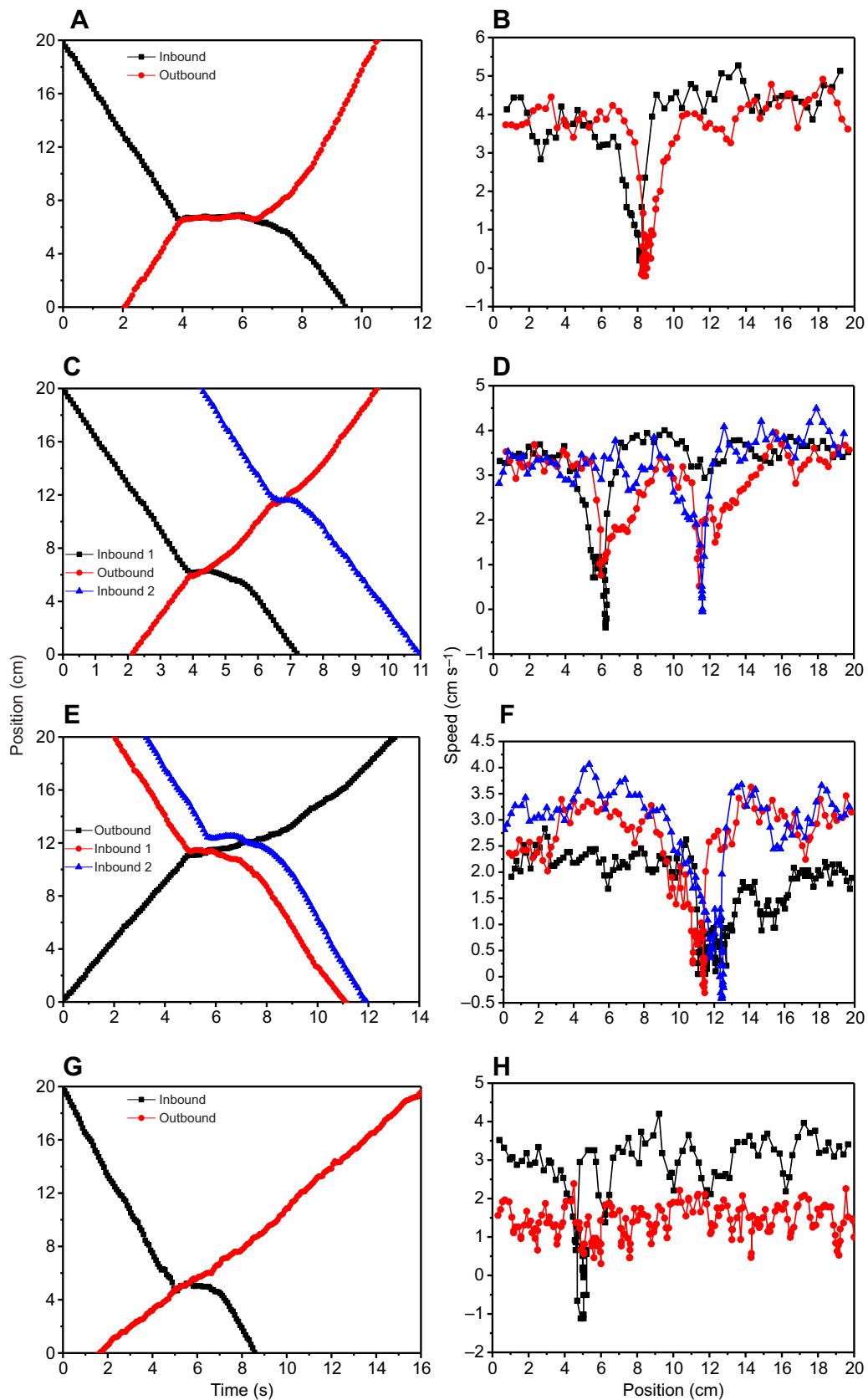


Fig. 6. Spatio-temporal graph for ant encounters (left) and the corresponding evolution of instantaneous speed with position (right). (A,B) Outbound and inbound ants encountering each other in the observation region. (C,D) Two discontinuous inbound ants encountering one outbound ant at different positions in the observation region; the outbound ant reduced its speed twice. (E,F) Two successive inbound ants and one outbound ant encountering each other; the outbound ant decreased its speed only once. (G,H) The outbound loaded ant moved with a steady speed in the observation region even though it encountered an inbound (loaded) ant.

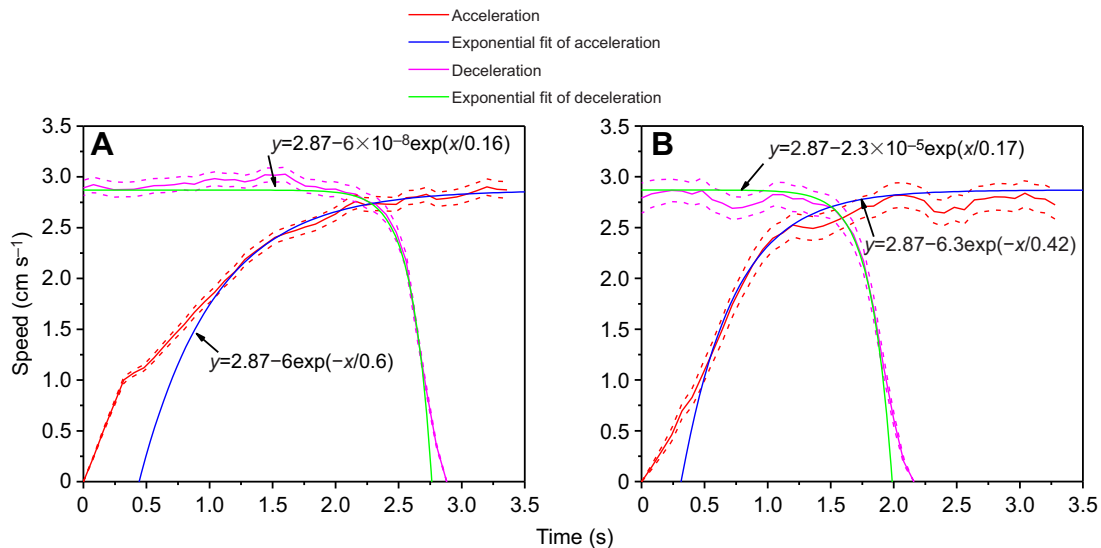


Fig. 7. Calibration of accelerations and decelerations from average time-dependent ant instantaneous speed. (A) Head-on encounters; (B) sudden stops. The fitted curves (blue for acceleration and green for deceleration) are given by Eqn 3 (see Results). The relaxation times were estimated as 0.6, 0.16, 0.42 and 0.17 s for acceleration and deceleration phases of the head-on encounters and sudden stops, respectively.

information exchange. Here, we calculated the reduction of movement efficiency due to head-on encounters as:

$$R = \frac{T_{\text{encounter}}}{T} - 1, \quad (4)$$

where $T_{\text{encounter}}$ (s) is the actual walking duration in the observation region when the head-on encounters happened (one unloaded ant encountered one or two discontinuous or successive ants). T (s) is the length of the observation region divided by the walking duration in the absence of head-on encounters. The difference between $T_{\text{encounter}}$ and T represents the time consumed by the head-on encounter process, and the ratio of $(T_{\text{encounter}} - T)$ to T indicates the reduction of movement efficiency, as expressed Eqn 4. The reduction in movement efficiency for encountering one ant, two discontinuous ants and two successive ants is presented in Fig. 8. It can be seen that the reduction in efficiency of one unloaded ant encountering an opposite-moving ant is 0.40 ± 0.21 . In addition, the reduction of movement efficiency for encountering two successive ants (0.53 ± 0.28) is significantly smaller than that when encountering two discontinuous ants (0.71 ± 0.4). Fig. 9 compares the reduction in efficiency of loaded and unloaded ants when they encountered one opposite-moving ant. For loaded ants, R was 0.138 ± 0.01 , which is less than that for unloaded ants (0.4 ± 0.21). There was a significant difference between loaded and unloaded ants by means of t -test (t -test: $T = -9.218$, $P < 0.05$). Therefore, head-on encounters have less influence on the movement efficiency of loaded ants.

DISCUSSION

In this ant nest relocation experiment, because of division of labor, the first ‘explorer’ worker went into the observed region at 2.23 min and then found the new nest. The first inbound ant appeared in the observation region at 9.73 min. However, the first loaded ant carrying a dead body appeared at 64.28 min, which was regarded as the beginning of nest relocation. Ants are eusocial insects; therefore, when they relocate their nest, the dead bodies of ants are also carried by workers from the old nest to the new one. It took 62.05 min for nest relocation using the accumulated pheromone trail. In a sealed

space, this is enough for pheromone accumulation because of its 30–60 min lifetime (Camazine et al., 2003). We assume that, during this period, a stable concentration of pheromone had been formed in the pipe and the safe state of the environment was ensured. Only under these conditions did the ants begin to relocate the nest. The path from the old nest to the new nest was a 1 m long, sealed transparent pipe, which is effective at reducing the evaporation of pheromone. The formation of a foraging or nest relocation trail would be expected to take more time in nature.

There are two basic types of traffic in nest relocation experiments: uni- and bi-directional. In these two traffic flows, the adaptation times (Jelić et al., 2012), i.e. the slope of the relationship of headway–speed in a strongly constrained regime, are the same, which means that ants have the same sensitivity to the distance headway not only for the tail of the preceding ant but also for the head of the opposite-moving ant. As interpreted in Cao et al. (2016) and Jelić et al. (2012), the intercept can be seen as a minimal individual space. The intercept in uni-directional traffic is 0.306,

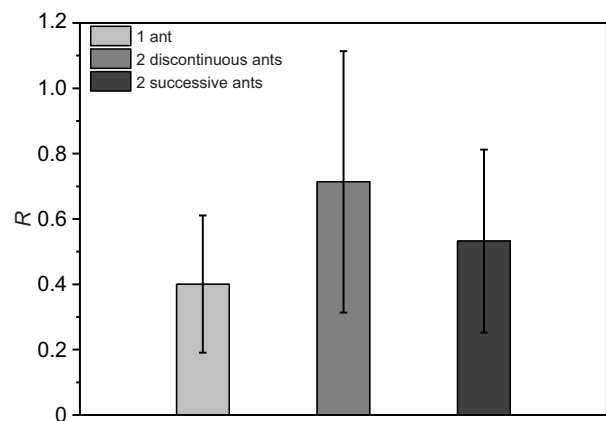


Fig. 8. Reduction in efficiency for one ant encountering one ant, two discontinuous ants or two successive ants in the observation region. The mean (\pm s.d.) reduction of movement efficiency (R) was 0.40 ± 0.21 , 0.71 ± 0.4 and 0.53 ± 0.28 , respectively.

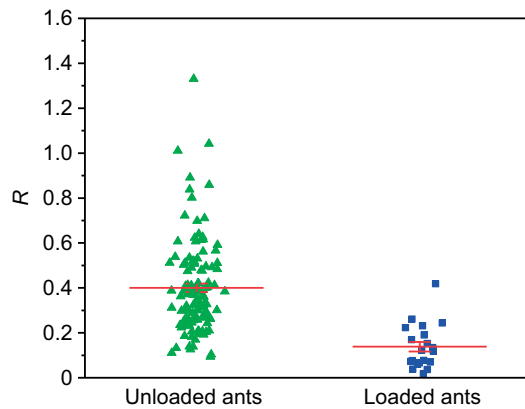


Fig. 9. Reduction in efficiency following the head-on encounter of one unloaded or one loaded ant with one unloaded ant. The red lines denote the average value of the reduction in efficiency (R) when one unloaded or loaded ant had a head-on encounter with one unloaded ant (0.4 and 0.138, respectively).

which is larger than that in bi-directional traffic (0.0723). The reason is that there is no overtaking behavior for following ants as found in John et al. (2009), and they decreased their speed with the distance headway. However, in bi-directional ant traffic, opposite-moving ants made head-on encounters and passed each other. In this way, when the speed was zero, the distance headway could approximate to zero before the ants gave way to each other. In addition, in bi-directional traffic, there is a weakly constrained regime. It is possible that the antennae of opposite-moving ants impacts their speed. In this work, we recorded three free speeds for unloaded ants: 2.87 cm s^{-1} in the observation region without following and head-on encounters, and 3 cm s^{-1} and 2.85 cm s^{-1} in the free regimes of uni-directional and bi-directional traffic, respectively. It was found that the free speed in uni-directional traffic (following behavior) is the greatest of these. This is because the following ants move with high speed owing to the high concentration pheromone deposited by the preceding one. In contrast, in the other two cases, the concentration of pheromone may be low relatively. Moreover, if the types of outbound pheromone (from the old nest to the new nest) and inbound pheromone (from the new nest to the old nest) are different, this would also result in a discrepancy in free speed.

In ant traffic, head-on encounters frequently occur in foraging (Farji-Brener et al., 2010). Similarly, in our experiment, not only head-on encounters but also sudden stops were observed. Sudden stops manifest as single individuals stopping abruptly and quickly without any external interference in the observation region. Both head-on encounters and sudden stops contain phases of deceleration and acceleration. The relaxation time of the deceleration phase is the same for head-on encounters and sudden stops. The reason is that ants are not harmed by collision and a collision avoidance strategy is therefore not required (Moffett, 1987). Furthermore, unlike the behavior of pedestrians, ants have the ability to stop and regain their speed rapidly. In this experiment, the relaxation time of deceleration was 0.16–0.17 s, which means that ants can stop quickly and control themselves effectively. In the acceleration phase, the relaxation time of head-on encounters is larger than that in sudden stops. This may be because in head-on encounters, opposite ants have to share the channel in the initial stage before they accelerate to their former speed, which limits the increase of speed. The relaxation time of deceleration is shorter than that of acceleration for both head-on encounters and sudden stops. The probable reason is that deceleration is a random or sudden procedure, which is mainly

determined by the ants' ability to control their bodies. In contrast, the acceleration phase is arbitrary without any urgency.

As plotted in Fig. 3, there was a significant discrepancy in speed of loaded and unloaded ants. The moving speed was influenced by the mass of the load that the ants carried (Burd and Aranwela, 2003) and their body size (Wang and Song, 2016). For some ants, head-on encounters cost them more time than carrying load in foraging. Taking *A. colombica* as an example, a quantitative analysis showed that the time cost for head-on encounters was twice as that for carrying things (Dussutour et al., 2009). In this experiment, the speed of loaded ants was smaller than that of unloaded ants as displayed in Fig. 3. However, the reduction of movement efficiency of loaded ants was smaller than that of unloaded ants when two opposite-moving ants encountered each other (see Fig. 9). One possible reason is that the higher mass of loaded ants means that their speed is less affected by head-on encounters. Another reason may be that loaded ants take less time for information exchange because of the influence of the dead body. When a loaded ant encountered an unloaded ant, it was observed that the unloaded ant stopped and gave way to the loaded ant (see Fig. 6G,H). This behavior of unloaded ants embodies the social attribute of collective cooperation, which can ensure high movement efficiency in nest relocation traffic.

Compared with bi-directional pedestrian and vehicle traffic, an ant with weak sight would not decelerate on the basis of vision as pedestrians or drivers would. Ants stop rapidly when they perceive the presence of others through their antennae. In the pedestrian experiment, when an interferer (pedestrian or obstacle) appeared in the planned route, the pedestrian adjusted their speed and direction to avoid collision (without physical contact) (Ma et al., 2010; Moussaïd et al., 2009). However, in ant bi-directional traffic, head-on encounters between opposite-moving ants are a common occurrence for information exchange, which takes ants 2.61 s. Thus, the decrease in speed due to the limits of space and time on information exchange lead to a reduction of movement efficiency. From this point of view, the pedestrian motion has higher efficiency than ant in bi-directional traffic.

In the observation region, one ant may meet one or more opposite-moving ants. The reduction of movement efficiency was 0.71 and 0.53 when one unloaded ant encountered two discontinuous ants and two successive ants, respectively. The reason for this smaller reduction of movement efficiency for encountering two successive ants is that the ant just decreased speed once and made a head-on encounter with the leader of the two successive ants, as the subsequent ant followed the leader one closely. In ant traffic, the following phenomenon is common, and it is beneficial to improving movement efficiency because of the attraction of the pheromone. In addition, the following ants can avoid head-on encounters with opposite-moving ants which gave way to them in bi-directional traffic. Thus, the following behavior for successive ants can improve movement efficiency in bi-direction traffic. Like workers of the black garden ant *Lasius niger*, they can maintain a high foraging efficiency in a narrow path with alternating clusters of inbound and outbound ants (Dussutour et al., 2005b). Furthermore, in the control experiment with pedestrians, the same phenomenon that clusters of pedestrians rather than single individuals passed the bottleneck from one side to the other was observed. After a period of time, pedestrians from the other side had a chance to pass this bottleneck (Helbing et al., 2005). Analogous to pedestrian or vehicle traffic in daily life, in some places, because of limitations of the environment, there are parts of the road that only one vehicle or pedestrian can pass at a time. In this case, the best way

to enhance transportation efficiency is by giving way to opposite-moving vehicles or pedestrians at a particular time, and then exchange. This embodies the importance of cooperation.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: W.S.; Methodology: Q.W.; Software: Q.W.; Formal analysis: Q.W.; Investigation: Q.W.; Resources: Q.W.; Data curation: Q.W.; Writing - original draft: Q.W.; Writing - review & editing: J.Z., W.S., S.L.; Visualization: J.Z.; Supervision: W.S., S.L.; Project administration: W.S.

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