Bi-directional movement characteristics of Camponotus

japonicus ants during nest relocation

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Highlight:

- 1) Nest relocation experiment of ants was conducted under illumination conditions.
- 2) Bi-directional traffic of ants in one-lane organization was observed and studied.
- 3) The relation of headway-speed indicates the same adaptation time for both uni-directional and bi-directional ant traffic.
- 4) Head-on encounters have influence on the movement efficiency of unloaded ants but less influence for loaded ants, which reflects the collective cooperation among ants.
- 5) Both in head-on encounter process and sudden stop process, the relaxation time of deceleration phase (0.16) is less than acceleration phase (0.6 for encounter and 0.42 for sudden stop).
- 6) For unloaded ants, reduction of movement efficiency of encountering two successive ants is 0.53 which is smaller than encountering two discontinuous ants 0.71.

Abstract:

Foraging and nest relocation forming a bi-directional traffic of outbound and inbound individuals in one-lane organization are two main activities in ants' life. In this paper, we conducted an experiment for nest relocation of loaded and unloaded ants, and some of them move back and forth between the old nest and the new one. In the experiment, we observed both uni- and bi-directional traffic flows of ants. The headway-speed relations indicate that the ants show the same sensitivity to the distance headway in both types of flows. For bi-directional traffic flow, head-on encounters and giving way behavior between opposite ants are common occurrence. It takes one unloaded ant 2.61 s to solve a head-on encounter with other unloaded one. Compared with unloaded ants, loaded ants have smaller moving speed, but are less likely to be impacted by head-on encounter. In observation region, both sudden stop and head-on encounter contained two phases, i.e. deceleration and acceleration were observed. Our analysis indicates that the relaxation time in deceleration process is less than that in acceleration process. The reduction of movement efficiency of encountering two discontinuous ants is larger than encountering two successive ants 0.18. This is owing to the absence of head-on encounter with following ants. Generally, this study investigates the bi-directional traffic of ants in experimental condition mainly and might inform the future studies of high-efficiency movement of collective behavior and traffic systems.

Key words: nest relocation, bi-directional ant traffic, head-on encounter, reduction of movement efficiency

1. Introduction

An ant colony, living 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). For different ants, they have different division of labor. Among them, the 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 mainly pattern in ants life (Hölldobler and Wilson, 1990). In recent years, the collective behavior of ants under emergencies was widely studied (Dias et al., 2013; Haghani and Sarvi, 2017; Wang et al., 2015). The experimental evidence of "Faster is Slower" effect is found in the evacuation experiment of ants under stressed conditions (Soria et al., 2012), but the jamming and clogging are 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 is differ from the most animals whose movements are uni-directional. The formation of foraging trail is benefit from pheromone that ants deposit it on the ground. This pheromone can attract the following ants to follow this trail and find the food resource ultimately, and the final destination of this trip is their nest (Norman and Hughes, 2016; Wilson, 1990). Before workers carry food to nest, the physical trails are built with a cleared trials, which can facilitate load transport and increase the rate of foraging efficiency (Bruce et al., 2017). Certainly, the time and energy of workers are needed to build physical trails and maintain it clear (Bochynek et al., 2017; Howard, 2001). Thus, the wider trails could take workers more time and energy, which decreases the rate of foraging efficiency.

As in vehicle traffic, some degree of lane segregation in ant traffic in spatial organization is observed, i.e. the trails of inbound and outbound are not intermingled completely. This is good for reducing the rate of head-on encounter. In some ant traffic, three-lane (trail divided into three lanes) is the common organization, such as army ant Eciton burchelli (Couzin and Franks, 2003). Compared with two-lane organization, three-lane would probably increase traffic flow due to less 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 pirating. However, due to the limitation of width of their trials, such as arboreal ants travelling on small branches or lianas, or litter ants walking in fallen branches or using structural guidelines (natural cracks, furrows or walls), one-lane organization occurs in ant trails (Dussutour et al., 2005a). Here, taking A. colombica as an example, the inbound and outbound trails are weak degree of lane separation (Dussutour, 2004). One hypothesis for explaining intermingled trail is that the high rate of head-on encounter observed in forging trail of A. colombica is benefit to information exchange and help 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 obstacle in it. Meanwhile, narrow path can maintain the pheromone in a high concentration, which can abstract following ants strongly for foraging. By this way, it is contributed to improve foraging efficiency. On the other hand, in the one-lane bi-directional traffic, the outbound ants make head-on encounter with loaded ants, but not with unloaded inbound ants. These head-on encounters result in the transfer of food between workers and this multistage of transport is called 'bucket brigades' (Anderson et al., 2002; Lee and Kim, 2017). This method may indicate that the foraging efficiency is greater in a narrow path than that in a wide path (Dussutour et al., 2007).

One-lane organization in ant traffic is common. Its foraging or nest relocation efficiency is higher than that in wide paths in which lane segregation occurs. In bi-directional ant traffic, head-on encounter, as the main pattern for opposite moving ants, plays an important role on 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 for spatial organization of trails. In this paper, the main goal is to study the bi-directional flow of ants (*Camponotus japonicus*) in a narrow path quantitatively. We conducted nest relocation experiment and the ants were stimulated to emigrate from their nest by changing the environment conditions (illumination and humidity) and supplying food.

2. Materials and methods

2.1 Insects

In this work, we performed a nest relocation experiment of *Camponotus japonicus* that is a species of black ant native to East Asia to investigate the collective behavior of ants. 427 worker ants from one colony (without queue) were collected in Shaanxi Province of China and transported to the laboratory. They were placed in a plaster box with a plastic lid on the top and the wall of box was painted with Fluon to prevent them from escaping. The box was kept at room temperature $(24\pm2^{\circ}C)$ under natural light/dark cycles with sufficient water and honey providing. When the experiment started, the ants had been raised in laboratory for three months and the average length of their bodies was 1.03 ± 0.11 cm (mean ± standard deviation).

2.2 Experimental setup

Fig. 1A shows the arena for the experiments. Two PP5 (polypropylene) boxes of the same size (41 cm long \times 29 cm wide \times 23 cm high) whose walls were 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 and its width allows two ants moving side by side. The old nest without food and water in it was placed in a well illumination environment, whereas the new nest was in a comfortable environment (dark and damp surroundings with adequate supply of food (honey) and water). In this way, the ants are easily driven to move from the old nest to the new one. A digital video camera with the frame rate of 25 fps placed over the pipe was used to record the whole process of the experiment. A 20 cm long area located at the middle of the pipe is selected as the observation region (see Fig. 1B). When the experiment began, we put the whole colony including dead bodies into the old nest.

2.3 Statistical analysis

We extracted trajectories of ants from the video sequences manually by tracking the head of ants. Through the 2D trajectories we firstly define the free speed $v_f(i)$ of *i*th ant by the following equation:

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

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

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

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

3. Results

3.1 Time, speed and distance headway in ant traffic

The old nest was in an abominable environment, whereas the new nest was suitable for ant to live. The strong contrast made ants relocate their nest from old one to new one spontaneously. When the ants were introduced into a fresh environment (old nest), they became active and moved in the whole box irregularly. The ones near the entrance of pipe spent less time to find the entrance and then arrived at the new nest through this pipe. The first ant entered the observation region 2.23 minutes later after the experiment began. With time elapsing, most of ants in the old nest were attracted by pheromones deposited by the pioneer ants and found the new nest finally as shown in Fig. 2. In order to exchange information with ants in old nest, ants in new nest returned to the old one. Thus, outbound and inbound ants encountered each other at somewhere of pipe. After a period of time, the stable concentration of pheromone was formed, so that workers began to carry the dead body to the new nest through the pipe. The first loaded ant appeared in the observation region at the 64.28th minutes. No inbound loaded ant was observed.

Because of different division of labor, some ants are just responsible for exploring trails with carrying nothing, i.e. some of unloaded ants. On the other hand, the main job for some others is carrying dead bodies from old nest to the new one in this nest relocation experiment, which is called as loaded ants. In the observation region, the free speed of unloaded ants was 2.87 ± 0.76 cm s⁻¹ while it was 2.22 ± 0.43 cm s⁻¹ for loaded ants as displayed in Fig. 3. There was significant difference in the average free speed between loaded and unloaded ants (T-test: T=8.32, P < 0.05).

In the process of nest relocation, there are two interactions observed among ants: following behavior for homodromous ants (uni-directional traffic) and head-on

encounters of opposite ants (bi-directional traffic). From the experiment of pedestrian (Cao et al., 2016; Jelić et al., 2012), it is found that the speed is dependent on distance headway with several linear relations. In this work, we also pay attentions to the relation of distance headway and speed. The available distance between neighboring ants is defined as distance headway, i.e. distance between the head of following ant and tail of preceding one in uni-directional traffic and distance of heads of two opposite moving ants in bi-directional traffic. In uni-directional ant traffic, several ants from the same direction passed the observation region only, and the relation 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 fitting curve, there are two linear regimes (strongly constrained regime and free regime) with different slopes for uni-directional traffic and three linear regimes (strongly constrained regime, weakly constrained regime and free regime) for bi-directional traffic. Compared the slope and intercept for uni-directional and bi-directional traffic flows, it is found that they have the same slopes (0.095, 0.094), while the intercept (0.306) of uni-directional traffic is larger than that (0.0723) in bi-directional traffic. In free regime, the average values of the speed are 3.0 cm s⁻¹ and 2.85 cm s⁻¹ for uni-directional and bi-directional traffic, respectively.

3.2 Head-on encounter

3.2.1 Trajectories

At the 9.73th minutes, the first inbound ant entered the observation region. Gradually, more and more inbound ants moved in the pipe, which induced the 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 moved in opposite directions encountered, they gave way to each other by shifting to the left or the right side. The trajectories clearly show that they present wavy form, and the remarkable detour emerged when the ants gave way for the ones from opposite side.

3.2.2 Deceleration and acceleration

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

speed from free speed to zero. Correspondingly, the acceleration phase is a process for the ants to 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, in which 23 ants encountered with the others. As shown in Fig. 6G, H, the speed of loaded ant did not decrease significantly like unloaded ants when they make head-on encounter with others. Thus, head-on encounter has less effect on motion of loaded ants. On one hand, loaded ants have a higher mass. Therefore, head-on encounters may lead to less effect on the speed of loaded ants due to inertia. On the other hand, loaded ants utilized their two strong jaws that are attached to the head and below their antennae, when they carry dead bodies (Borror et al., 1989). The dead body with large size may affect the function of antennae in some degree. Meanwhile, the dead body also resulted in the process of antennae contact, i.e. information exchange, was not observed clearly. In addition, without external interference, loaded ants did not stop suddenly.

As shown in Fig. 6, the deceleration and acceleration are the basic phases for the encountered ants. In terms of the behavior of head-on encounter with opposite ants, we calculated their movement characteristics, such as the evolution of speed with time in deceleration and acceleration phases, by averaging these two phases. In deceleration phase, the zero time is a certain time that all the recorded ants moved with free speed, and the time that speed of ants reduced to zero is the same. For the acceleration phase, the speed equaling to zero was the zero time, but in next time step, their speed was larger than zero. In Fig. 7A, it shows the results of the deceleration and acceleration phases for head-on encounter process and the exponential curves. As shown in Fig. 7A, the deceleration and acceleration curves conform to exponential distribution. The exponential function is expressed as follow:

$$v = v_f + A * \exp(-t/\tau) \tag{3}$$

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

In observation region, it is also observed in the video that some ants stopped suddenly without any exotic interference and then started moving again. In this case, the deceleration and acceleration phases are included as illustrated in Fig. 7B. The results show that the mean relaxation time of deceleration phase is 0.17 s and $\tau = 0.42$ s for the acceleration phase. Comparison of head-on encounter process and sudden stop shows the mean relaxation time of deceleration phase is similar, however, ants took less time to restore their speed from zero in the sudden stop condition.

3.2.3 Reduction of movement efficiency

In the foraging performance of ants, head-on encounter between workers is common in ant traffic. The behavior of head-on encounter reduced the motion speed, thus it diminished the movement efficiency (Burd and Aranwela, 2003). In this work, the reduction of movement efficiency caused by head-on encounter is studied quantitatively. Firstly, the head-on encounter process was defined as the time elapsed from the contacting of antennae of two opposite ants to the completely separation of them. When an unloaded ant encountered one opposite ant, the average walking time is 2.61 ± 1.13 s. When it encounters two successive ants, it takes 4.24 ± 1.52 s. From this result, it shows encountering two successive ants would take less walking duration in head-on encounter process and improve the movement efficiency is 18.9%. As observed in the observation region, ants encountering with others reduced their movement efficiency in view of reduction of speed and information exchange mainly. Here, we calculate the reduction of movement efficiency due to the head-on encounter with formula expressing as:

$$R = \frac{T_{encounter}}{T} - 1 \tag{4}$$

where $T_{encounter}$ (s) is the actual walking duration in observation region when the head-on encounters happened (one unloaded ant encountered one or two (discontinue or successive) ants). T (s) equals to the length of the observation region divided by the walking duration in a freeway in absence of head-on encounter process. The difference of $T_{encounter}$ and T represents the time consuming on head-on encounter process, and the ratio of $(T_{encounter}-T)$ and T indicates the reduction of movement efficiency, as expressed Eqn 4. The reduction efficiency for encountering one, two discontinuous ants and two successive ants is presented in Fig.8. It is shown that the reduction efficiency of one unloaded ant encountering an opposite ant is 0.4±0.21. In addition, the reduction of the movement efficiency for encountering two successive ants $(0.53\pm0.28s)$ is smaller than encountering two discontinuous ants $(0.71\pm0.4s)$ significantly. Fig.9. compares the reduction efficiency of loaded and unloaded ants when they encountered one opposite ant. For loaded ants, it is 0.138±0.01s which is less than unloaded ant with 0.4±0.21s. There is a significant difference between loaded and unloaded ants by means of T-test (T-test: T=-9.218, P < 0.05). Therefore, head-on encounter has less influence on loaded ants in movement efficiency.

4. Discussion

In the nest relocation experiment of ants, because of division of labor, the first worker as explorer went into the observed region at the 2.23th minutes and then found the new nest. The first inbound ant appeared at the observation region was at the 9.73th minutes. However, the first loaded ant started carrying dead body was at the 64.28th minutes, which was regarded as the beginning of the nest relocation. Ants are eusocial insects, therefore, when they relocate their nest, the dead body was also

carried by workers from the old nest to the new one. It took 62.05 minutes on the accumulation of pheromone trail for nest relocation. In a sealed space, it is enough for pheromone accumulation as a result of 30-60 minutes lifetime of pheromone (Camazine et al.). It can assume that during this period, the stable concentration of pheromone had been formed in the pipe, and the environment being in a safe state was ensured. Only under these conditions did the ants begin to relocate nest. The path from old nest to new nest is a sealed transparent pipe with 1 m long, which is effective to reduce the evaporation of pheromone. By parity of reasoning, the formed of foraging or nest relocation trail would take more time in nature.

There are two basic traffics: uni- and bi-directional traffics in nest relocation experiment. In these two traffic flows, the adaptation times (Jelić et al., 2012), i.e. the slope of relation of headway-speed in strongly constrained regime, are the same, which means ants have the same sensitivity to the distance headway not only for the tail of preceding ant but also the head of opposite ant. As interpreted in Refs. (Cao et al., 2016; Jelić et al., 2012), the intercept can be seen as a minimal individual space. The intercept in uni-directional traffic is 0.306 that 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 Ref. (John et al., 2009), and they decreased their speed with the distance headway. However, in bi-directional ant traffic, opposite ants made head-on encounter and passed each other. By this way, when the speed is zero, the distance headway could be approximate to zero before giving way for each other. In addition, in bi-directional traffic, there is weakly constrained regime. It is perhaps that the antennae of opposite ants impacts their speed. In this work, we recorded three free speeds for unloaded ants: one is 2.87 cm s⁻¹ in observation region without following and head-on encounter behaviors, and the other two free speeds are 3 cm s⁻¹ and 2.85 cm s⁻¹ in free regimes of uni-directional and bi-directional traffics, respectively. It was found that the free speed in uni-directional traffic (following behavior) is the largest one. This is because that the following ants move with high speed owing to the high concentration pheromone deposited by preceding one. On the contrary, in the other two cases, the concentration of pheromone may be low relatively. Moreover, if the types of outbound pheromone (from old nest to new nest) and inbound pheromone (from new nest to old nest) are different, this would also result in the discrepancy in free speed.

In ant traffic, head-on encounters occur in foraging frequently (Farji-Brener et al., 2010). Similarly, in our experiment, not only head-on encounter but also sudden stop was observed. For the sudden stop, it manifests as some single individuals stopped suddenly and quickly without any exoteric interference in the observation region. Both head-on encounters and sudden stop contain the phases of deceleration and acceleration. The relaxation time of deceleration phase is the same for head-on encounters and sudden stop. The reason is that ants are not harmed by collision and the collision avoidance strategy is not needed for them (Moffett, 1987). Furthermore, unlike the behavior of pedestrian, ants have the strong ability to stop and regain their speed rapidly. In this experiment, the relaxation time of deceleration is 0.16~0.17 s that means ants can stop quickly and control themselves effectively. In the

acceleration phase, the relaxation time of head-on encounter process is larger than that in sudden stop process. It is perhaps that in head-on encounter process, opposite ants have to share the channel in the initial stage before they accelerate to former speed, which limit the increase of speed. The relaxation time of deceleration is less than acceleration phase for both head-on encounters and the sudden stop. The probable reason is that deceleration is a random or sudden procedure, which is determined by their ability to control their bodies mainly. On the contrary, acceleration phase is arbitrary without any urgency.

As plotted in Fig. 3, there is significant discrepancy on speed for loaded and unloaded ants. The moving speed was influenced by the mass of load that ants carried (Burd and Aranwela, 2003) and their body size (Wang and Song, 2016). Actually, for some ants, head-on encounters cost them more time than carrying load in foraging. Taking A. colombica as an example, a quantitative analysis shows that the time costing at head-on encounters is twice as high as spending in carrying things (Dussutour et al., 2009). In this experiment, the speed of loaded is smaller than unloaded as displayed in Fig. 3. However, the reduction of movement efficiency of loaded ant is smaller than unloaded ant when two opposite ants encountered (see Fig. 10). One possible reason is that a higher mass of loaded ants make them less effect on speed by head-on encounters. Another reason may be that loaded ants take less time on information exchange due to the influence of dead body. Once a loaded ant encountered an unloaded ant, it was observed that unloaded ant stopped and gave way to loaded ant (seeing Fig.6 (G, H)). This behavior of unloaded ants embodies the collective cooperation in social attribute, which can ensure high movement efficiency in nest relocation traffic.

Compared with bi-directional pedestrian and vehicle traffic, the ant with weak sight, would not decelerate on the base of vision as pedestrians or drivers. They stop rapidly when they perceive the presence of others through their antennae. In the pedestrian experiment, when a interferer (pedestrian or obstacle) appeared in the planned route, 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 ants are a common occurrence for information exchange, which takes ants 2.61 s. Thus, speed decreasing due to the limitation of space and time consumption on information exchange lead to the 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 passing this region may meet one or more opposite ants. Reduction of movement efficiency is 0.71 and 0.53 when one unloaded ant encounters two discontinuous ants and two successive ants, respectively. The reason of small reduction of movement efficiency for encountering two successive ants is that the ant just decreased speed by one time and made head-on encounters with the leader one of successive ants since the followers following the leader one closely. In ant traffic, the following phenomenon is common, and it is beneficial to improving movement efficiency due to the attracting of pheromone. On the other hand, the following ants can avoid head-on encounter with opposite ants who gave way to them in bi-directional traffic. Thus, the following behavior for successive ants can improve the 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 with alternating clusters of inbound and outbound ants (Dussutour et al., 2005b). What's more, in the control experiment of pedestrians, it observed the same phenomenon that clusters of pedestrians rather than single individuals passed the bottleneck from one side to the other. After a period of time, pedestrians from the other side had a chance to pass this bottleneck (Helbing et al., 2005). Analogous to pedestrians or vehicle traffic in daily life, in some places, due to the limitations of environment, there is one road that only one vehicle or pedestrian passed at the same time. In this case, the best way to enhance transportation efficiency is giving way for opposite vehicles or pedestrians in a certain time, and then exchange. This embodies the importance of cooperation.

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Figures

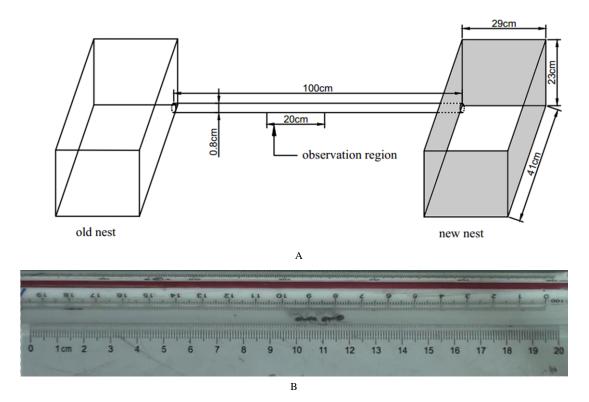


Fig. 1 Schematic diagram of experimental setup. (A) Two same size boxes were connected by a transparent pipe, and the observation region is 20 cm at the middle part of this pipe. (B) A snapshot shows that outbound and inbound ants made head-on encounter in observation region.

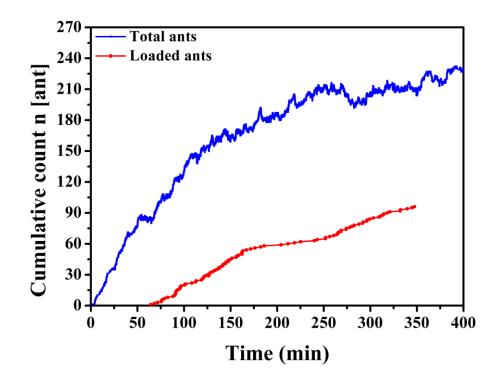


Fig.2 Cumulative count of ants moving from old nest to new nest. The blue curve records the total ants in the nest relocation experiment, in which outbound and inbound ants are included. Red line just calculates the outbound ants who carried dead bodies.

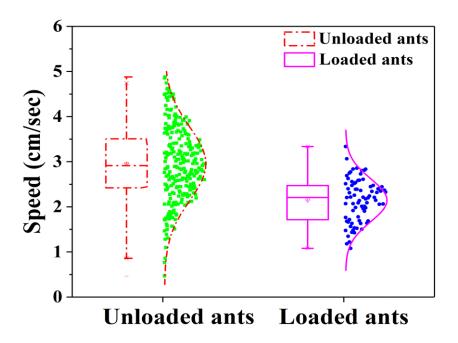


Fig.3 Distribution of speeds of ants. Two box charts show the average speeds of ants for unloaded (red) and loaded ants (magenta), and the green and blue dots represent the free speed of single ant of unloaded and loaded ants. Red dashed line and magenta line indicate the distribution of free speed for unloaded and loaded ants.

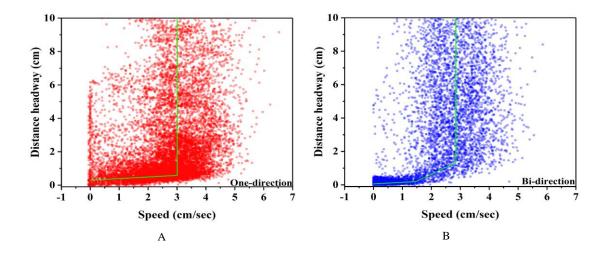


Fig.4 Scatter diagrams (red and blue dots) and linear fitting curve (green line) of headway-speed relation for one-directional traffic (A) and bi-directional traffic (B). The single dots represent the instantaneous speed of ants for corresponding distance headway. In the constrained regime, the linear curve is according to the peak values of distance headway for each bin (Δv =0.1).

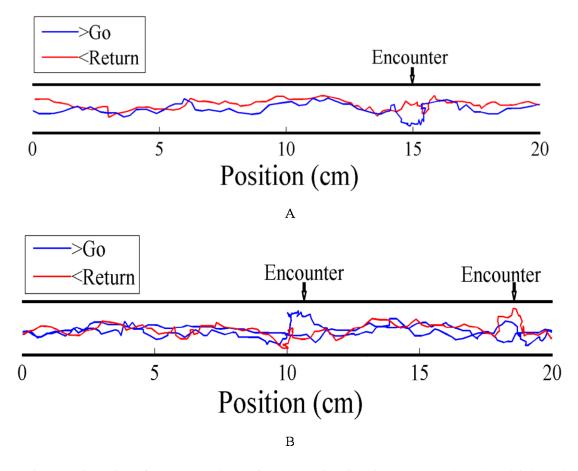


Fig.5. Trajectories of encountered ants from opposite directions. (A) Outbound and inbound ants from opposite directions encountered at observation region. (B) Two outbound ants and one inbound ant encountered at different position.

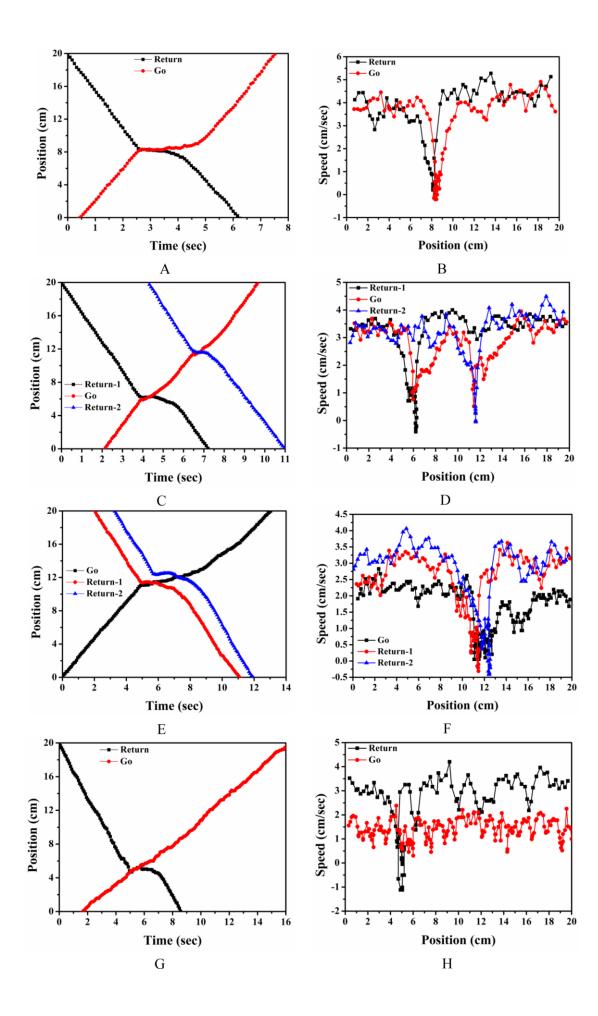


Fig.6. Spatio-temporal graph for encountered ants (A,C,E,G) and the corresponding evolving of instantaneous speed with position (B,D,F,H). (A, B) Outbound and inbound ants from different directions encountered in observation region. (C, D) Two discontinuous inbound ants encountered with one outbound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

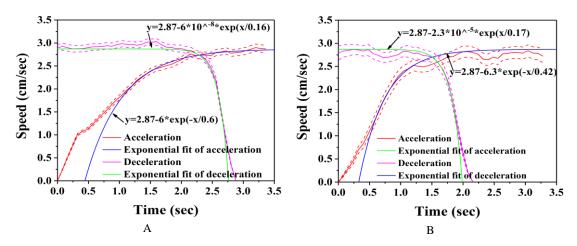


Fig.7. Calibration of accelerate (red line) and decelerate (magenta line) behavior in the light of the average time-dependent ant instantaneous speed for the processes of (A) head-on encounter and (B) sudden stop. The fitted curve (blue for acceleration and green for deceleration) are given by equation (3). The relaxation times were estimated as 0.6, 0.16, 0.42 and 0.17 for acceleration and deceleration phases of head-on encounter and acceleration and deceleration phases of sudden stop, respectively.

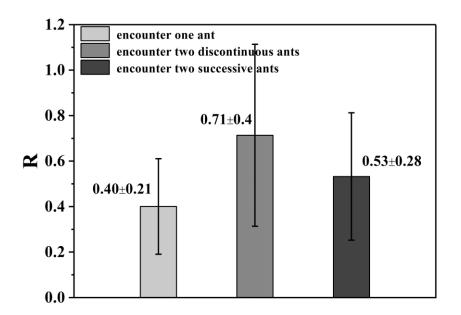


Fig.8. Reduction efficiency for one ant encounters one (light gray), two discontinuous ants (gray) and two successive ants (dark gray) in observation region. The average reduction of movement efficiency and standard deviation (error bar) are 0.4 ± 0.21 , 0.71 ± 0.4 , and 0.53 ± 0.28 , respectively.

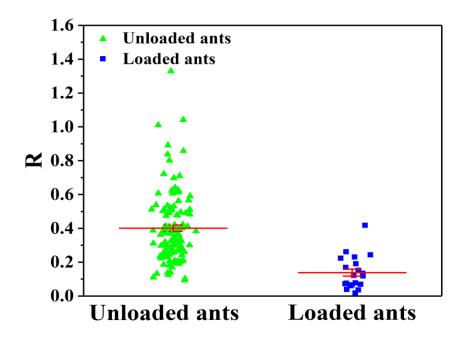


Fig.9. Reduction efficiency of head-on encounter for one unloaded (green triangle) and no one loaded ants (blue square) encountered one unloaded ant. The red lines denote the average value of reduction efficiency when one unloaded and loaded ant made head-on encounter with one unloaded ant, which are 0.4 and 0.138.