Route reassessment by transporter ants improves speed and directional accuracy of cooperative transport in *Formica japonica*

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Abstract

Encircling cooperative transport in ants is categorized into coordinated and uncoordinated types. Coordinated cooperative transport is considered to be advantageous for ants because it transports food quickly without creating a deadlock. Contrarily, uncoordinated transport is slow and frequently becomes deadlocked. This study assessed the characteristics of uncoordinated cooperative transport, which has scarcely been studied before, through experiments performed on *Formica japonica*. Based on our experiment and analysis, we report that the transport speed remains unchanged with the number of transporters. We also found that pulling transporter ants often left the food item transiently as the transport speed decreased, and then went back to the item. Upon rejoining transport, the transport speed increased. This is presumably because the ants gain navigation information during the period that they leave the food. We propose that this ‘route reassessment’ behavior is important for transport coordination and navigation in *F. japonica*.

Keywords Ants · Collective behavior · Foraging behavior · Coordination · Cooperative transport · Navigation · Route reassessment · Backward homing

Introduction

Ants use two strategies for collecting large food items: one method is that each individual transports a part of a food item after having dissected it, and the other method is that multiple individuals carry an intact food item without dissecting it (Yamamoto et al. 2008). The latter strategy is called “cooperative transport” and constitutes a collective behavior. In this study, we defined cooperative transport as the grasping and moving of a food item by two or more workers, which is consistent with a previous study (McCreery and Breed 2014). Some species perform cooperative transport, while other closely related species do not (Hölldobler and Wilson 1990; Yamamoto et al. 2008; Czaczkes

and Ratnieks 2013). Therefore, the occurrence of cooperative transport may be due to convergent evolution of group behavior.

Recently, cooperative transport has been generally classified into at least three types: encircling coordinated, encircling uncoordinated, and “other” types (Czaczkes and Ratnieks 2013; McCreery 2017). In encircling coordinated cooperative transport, individuals encircle the food item and quickly transport it without deadlock, which is defined by an acute reduction in transport speed or a complete halt in transport. In contrast, uncoordinated cooperative transport is characterized by frequent and long-lasting deadlocks and a slower transport speed (Czaczkes and Ratnieks 2013). The “other types” of cooperative transport include the forward-facing (Franks 1986) and chain types (Peeters and De Greef 2015), the former of which perform cooperative transport effectively. In this study, we focus on the difference between the coordinated and uncoordinated types of cooperative transport. In this manuscript, hereafter, coordinated transport refers specifically to coordinated encircling transport.

Coordinated cooperative transport requires a high degree of order to achieve a consensus on the direction of transport; this process has thus received much attention as a potential model for collective decision-making (Gelblum et al.

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2015; McCreery et al. 2016). Quantitative analyses have provided information on the fundamental features of coordinated cooperative transport; for example, in several species, transport speed has been demonstrated to increase with the number of individuals participating in transport (Buffin and Pratt 2016; Cerdá et al. 2009; Czaczkes et al. 2010; Gelblum et al. 2015), and ants that play a role in steering are essential for pivoting food items in *Pheidole oxyops* (Czaczkes and Ratnieks 2010). Gelblum et al. (2015) claimed that cooperative transport in *P. longicornis* involves a division of labor consisting of individuals taking one of three roles: controlling the direction of transport (newly attached ant), providing force (puller), and reducing friction (lifter). Newly attached ants, which correct the direction of movement of the group for a few seconds, are added continuously to the carried item from the nest until the transported item reaches the nest. The most recently attached ant takes over the role of controlling the direction of transport from the previous one.

By contrast, little information is available on uncoordinated cooperative transport, i.e., transport characterized by frequent and long-lasting deadlocks because members cannot form a strong consensus. Accordingly, Traniello and Beshers (1991) reported that in *F. pallidefulva*, the transport speed showed no significant correlation with the average group size; however, the time resolution of the analysis was low. It has been assumed that deadlocks are solved via random changes in the location at which each individual grasps the food item (Czaczkes and Ratnieks 2013; Sudd 1960, 1965). In *Myrmica rubra* and *Formica lugubris*, rearrangement of the body position by the ants “swinging” their body reduces friction against the ground and can result in deadlocks being broken (Sudd 1965). Cooperative transport in *Solenopsis invicta* falls into deadlock frequently, and thus is categorized as uncoordinated transport; however, this method of transport still takes a more direct route than would individual transport in this species (Wang et al. 2016).

To reveal factors that could improve the efficiency of cooperative transport, McCreery (2017) compared uncoordinated and coordinated transport across species. In species exhibiting coordinated (*P. longicornis*) and uncoordinated (*Formica obscuripes*, *Formica pallidefulva*, and *Formica podzolica*) types of cooperative transport, the relationship between coordination parameters (sinuosity and success rate) and persistence (duration of contact with food) was investigated. Sinuosity is the ratio of the total path length to the shortest path length, and success rate is the rate of success of cooperative transport. The results of the study suggested that high persistence is correlated with a greater degree of coordination. There is presumably some decision-making function performed to solve a deadlock, even in uncoordinated cooperative transport. It is important to further study uncoordinated transport; it can be considered a simple system of cooperative transport and may, thus,

allow for an understanding of the evolution of cooperative behaviors.

In this study, we used *Formica japonica* Motschoulsky, 1866 as a model of uncoordinated cooperative transport. This species is known for performing cooperative transport during foraging (Yamamoto et al. 2008). This ant primarily uses visual information rather than pheromones for foraging and homing to the nest (Fukushi and Wehner 2004). We initially performed experiments to investigate the quantitative features of uncoordinated transport, including the relationship between the transport ability and the number of transporters. It should be noted that our analysis goes further than the previous study of *F. pallidefulva* (Traniello and Beshers 1991) by having a higher time resolution with more detailed and quantitative analyses and also by adopting an index of transport efficiency (see below). Because heavy food items need to be pulled, we focused on the pulling ants. Upon observing the ants’ behaviors, we found that a pulling individual sometimes released the food transiently during cooperative transport in *F. japonica*. This looked similar to behaviors that have been observed during individual transport, known as the “foodless search loop” and “peeking” in *Cataglyphis fortis* and *Cataglyphis velox*, respectively (Pfeffer and Wittlinger 2016; Schwarz et al. 2017). We termed this behavior in *F. japonica* “reassessment,” because the trajectory of the reassessing ant did not form a loop, and the duration of the reassessment (several tens of seconds) was longer than that of peeking (several seconds). After peeking and the foodless search loop, the accuracy of transport increased, as it did after the reassessment behavior. It should be noted that navigation during backward-walking is considered a complicated system. This is because that during the shift from forward- to backward-walking, the transporter needs to correct information about the relative position of a landmark to themselves. Although peeking behavior updates the course direction using the celestial compass, reassessments were performed under conditions with no artificial landmarks or sunlight. To understand the navigation method during backward-walking in cooperative transport, we quantitatively analyzed the reassessment process.

Materials and methods

Experimental setup

Two colonies (A and B) of *F. japonica*, each made up of a queen and 200–500 workers with larvae and brood, were used between June and August 2016 and 2017, respectively. In more detail, during June 2014 (A) and 2015 (B), after a nuptial flight, each queen was collected from Chiba Prefecture, after which ~130 pupae were introduced into colony A or B during June 2015 or 2016, respectively. The

pupae were introduced from other colonies to increase the sizes of the experimental colonies. It seems probable that all workers derived from the additional colony had died before starting this experiment, because the lifespan of a worker after emergence is shorter than 1 year (Higashi 1979). They were incubated at 25 ± 1 °C with a photoperiod of 12 h light:12 h dark. Their nests were established in plastic cases, in which the floor was covered with plaster. Except for during our experiment, the colonies were fed mealworms and sugar water twice a week. A plastic box of 300 mm width $\times$ 100 mm height $\times$ 200 mm depth was used as an experimental space. To prevent ants from climbing out, the side faces were coated with Fluon (Fluon PTFE, Asahi Glass Co. Ltd., Tokyo, Japan), and the floor was covered with copier paper, which was replaced on the day of every experiment. The nest and workers were moved from the incubator to the experimental space and allowed to adapt for 30–60 min before the experiment. At the beginning of the experiment, a piece of normal ham (10×10 mm, mean weight of 0.14 mg with a standard deviation of 0.018; CGC Japan Co. Ltd., Tokyo, Japan) was placed in the space. A single individual was able to transport food of this size by pulling. It should be noted that neither a single individual nor multiple individuals were able to transport food that was four times larger in size (20×20 mm).

The movement of ants to transport this food item was recorded with a video camera (iVIS HF R42; Canon, Tokyo, Japan) for the duration of the experiment (until the food reached the nest). We then converted the videos (MOV files) to TIFF stack files (10 fps 8-bit grayscale) using QuickTime 7 Pro (Apple, Cupertino, CA, USA). The centroid of a cropped image, which consisted of a food item and the attached ants, was defined as the position at the indicated time. The trajectory of the food item and the number of ants attached to it at a particular time were extracted from the images using ImageJ 1.51p (<https://imagej.nih.gov/ij/>). The number of trials for both colonies was 15.

Speed

We defined the sequence of food transport from beginning to end (reaching the nest) as a single “trial”. To quantitatively evaluate the transport ability, we used instantaneous transport speed (hereinafter called “transport speed”), “approach speed”, and “transporter number” as indices. The position of the food was recorded every 1 s to avoid measurement noise when both speeds were calculated. The transport speed (mm/s) at a certain time point was calculated from the movement of the center of the food (see Fig. S1a). The approach speed (mm/s) at a time point was calculated from the variation in the distance from the food to the nest over a period of one second (see Fig. S1a). Thus, it was represented as either a positive or negative value: when the food

moves in the opposite direction from the nest, the approach speed adopts a negative value. It should be noted that the approach speed represents a product of transport speed and accuracy in the direction of transport. The number of transporters was defined as the number of individuals in contact with the food, excluding the ants that ride on the food. The transporter number at a time point was defined as the median value of the number of transporters during the 10 frames (1 s). The representative value of each trial was the median speed of that trial.

Reassessment

To investigate the effect of reassessment on the accuracy, we used three more indices, moving distance, straightness, and angle error from the nest direction (hereinafter called “angle error”) for a 5-s duration before the releasing event and that after the retouching event (measured with “*trajR*,” McLean and Skowron Volponi 2018). The moving distance in a certain trajectory is the distance from the starting position to the goal position (see Fig. S1b). Straightness is the moving distance divided by the sum of the path length, ranging from 0 to 1. When the trajectory of transport is taken as a straight line, the straightness is 1 (see Fig. S1b). The “angle error” was calculated as follows: (i) we resampled the trajectory to a fixed length (0.5 mm; see Fig. S1c). (ii) The angle between the direction to the nest and that to the next position was calculated at each resampled position (see Fig. S1d). (iii) The median value of calculated angles was taken as the angle error from the nest direction index. Only when the angle error was calculated, we excluded the trajectories in which the total path length was shorter than 2 mm.

Statistical analysis

All statistical analyses were performed using R ver. 3.6.1 (R Core Team 2019). To test the relationship between the approach and instantaneous transport speeds and the transporter number, we used a linear mixed model (LMM) fitted by the restricted maximum likelihood method with “*lme4*” (Bates et al. 2015). The approach speed and transport speed were introduced as response variables. The fixed effects were “transporter number” and “colony” (A versus B). In addition to these effects, “colony $\times$ transporter number” was introduced as an interaction term. The random effect was the trial.

To investigate the changes in approach and transport speed before and after reassessment behaviors, the Wilcoxon signed-rank test was used with “*exactRankTests*” (Hothorn and Hornik 2017). We tested for homogeneity of angle error with the Watson–Wheeler test for homogeneity with “*circular*” data (Agostinelli and Lund 2017). To test the deviation

from the normal distribution, we used the Shapiro–Wilk test ($p > 0.05$).

Results

Relationship between number of transporters and speed

As mentioned above, the efficiency and speed of coordinated cooperative transport have previously been reported to increase with an increase in transporter number (Buffin and Pratt 2016; Cerdá et al. 2009; Czaczkes et al. 2010; Gelblum et al. 2015), while little is known for uncoordinated transport. Thus, we initially analyzed if the efficiency or speed of transport in *F. japonica* was dependent on the number of food-attaching individuals by examining the relationship between the number of simultaneously food-attaching transporters and the approach and instantaneous transport speed in *F. japonica* (Fig. 1) using two colonies. The definitions and measurements of instantaneous transport and approach speeds are described in the “Materials and methods”. As shown in Fig. 1a, it was not evidence that the (instantaneous) transport speed increased with the transporter number (Table 1). Detailed analysis with the LMM method

(“Materials and methods”) also supported this result. For the approach speed (Table 2), there was an increase in speed with an increase in transporter number in one of the colonies (colony A). This conditional effect will be discussed below, considering the effect of route reassessment.

Reassessment improves transport

From further observations, we frequently found that an individual pulling a food item improved the transport efficiency with the following series of behaviors: (i) a pulling individual leaves the food item temporarily, (ii) walks around the subject, (iii) returns to the food, and (iv) begins pulling the item again (we named this series of behaviors “reassessment;” see Fig. 2; Supplementary file 2). Here, we define a “pulling individual” as an individual in contact with the side of the food toward the moving direction and directing its abdomen in the same direction. Pulling individuals were tracked by eye to improve the accuracy. We define the time points when a pulling individual leaves the food as “releasing events” and those when it bites the food again as “retouching events.”

Reassessment was similar to the previously described peeking and foodless search loop behaviors of *C. velox* and *C. fortis*, respectively (Schwarz et al 2017; Pfeffer

Fig. 1 Approach and instantaneous transport speeds with different number of transporters. **a** Approach speed with different numbers of transporters. **b** Instantaneous transport speed with different numbers of transporters. The plot represents the median value of speed in a trial. The numbers of replicates were $n=21, 26, 30, 29, 27, 24, 21, 20, 14, 9, 6, 4, 2$, and 2 for experiments with transporter numbers of 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, and 14, respectively. Red bars show the standard deviation and red rhombuses represent the means of the median speed values

Table 1 Summary of the linear generalized mixed effect model (LMM) in instantaneous transport speed

Fixed effect						Random effect	
Parameter	Estimate	SE	df	t value	p value	Parameter	SD
Intercept ^a	1.14988	0.10649	116.97948	10.798	<0.001	Residual	0.4127
Transporter number	0.02501	0.02105	225.32782	1.188	0.236	Trial	0.2177
Colony ^b	-0.30134	0.14395	103.67551	-2.093	0.0388		
Transporter number × colony ^c	-0.01785	0.02402	223.69907	-0.743	0.4583		

Instantaneous transport speed depending on the transporter number and colony. Parameters are described in the “Materials and methods”

^aIntercept of regression line

^bCategorical fixed effect. In colony A, colony = 0; in colony B, colony = 1

^cInteraction term

Table 2 Summary of the linear generalized mixed effect model (LMM) in approach speed

Fixed effect						Random effect	
Parameter	Estimate	SE	df	t value	p value	Parameter	SD
Intercept ^a	0.34537	0.10436	114.01742	3.309	0.00125	Residual	0.4138
Transporter number	0.05604	0.02102	225.55528	2.665	0.00825	Trial	0.2008
Colony ^b	-0.01611	0.14078	99.90439	-0.114	0.90914		
Transporter number × colony ^c	-0.06664	0.02400	223.73012	-2.776	0.00597		

Approach speed depending on the transporter number and colony

^aIntercept of regression line

^bCategorical fixed effect. In colony A, colony = 0; in colony B, colony = 1

^cInteraction term

Fig. 2 Values indicating speed around each reassessment event (each of 10 s, before and after the event) were collected. **a** Approach speeds before and after retouching and releasing events. **b** Approach speeds before and after retouching events. **c** Instantaneous transport speed before and after retouching and releasing events. **d** Transport speed

before and after releasing and retouching events. Blue lines represent the mean value and error bars are standard deviation. The number of reassessments and trials summarized in this figure are 80 and 25, respectively

and Wittlinger 2016). These similar behaviors improve the accuracy of transport, while they are not exactly the same as the behavior described in this study. We assumed that reassessment led to the renewal of route information to improve transport efficiency. To confirm this assumption, we initially investigated changes in the approach and transport speeds before and after “releasing” and “retouching” events of reassessment (Fig. 2). Values indicating the speed around each reassessment (10 s each, before and after the event) were collected. As shown in Fig. 2a and c, the approach and transport speeds decreased before releasing events. We compared the median speed within 5 s before a releasing event with that after the retouching event. The speed after the retouching events was significantly larger than that before the releasing event (Wilcoxon signed-rank test: transport speed: $V=676$, $p<0.001$, approach speed: $V=479$, $p<0.001$). As shown in Fig. 2b and d, the approach and transport speeds significantly increased immediately after a retouching event (Wilcoxon signed-rank test: transport speed, $V=32$, $p<0.001$; approach speed: $V=265$, $p<0.001$), then decreased gradually. We cannot determine the casual link between a decrease in speed and the occurrence of reassessment. Furthermore, we compared the accuracy of transport before a releasing event with that after a retouching event using three more indices: moving distance, straightness, and angle error. The moving distance and straightness after a retouching event were significantly higher than that before the releasing event (Fig. 3; Wilcoxon signed-rank test: moving distance, $V=2534$, $p<0.001$; straightness, $V=2728$, $p<0.001$). The distribution of angle error before the releasing event was also significantly different from that after the retouching event (Fig. 4; Watson–Wheeler test,

Fig. 3 Accuracy of transport before and after reassessment. **a** Moving distance. **b** Straightness index. “Before release” represents the indices in the 5 s before a releasing event. “After retouch” represents the indexes in the 5 s after the retouching event. “After double” means the indices in the 5 s after the retouching event when another reassessing ant came into contact with the food. The number of replicates of “Before release,” “After retouch,” and “After double” were 76, 76, and 4, respectively. “Before release” and “After retouch” were tested with the Wilcoxon signed-rank test. “After retouch” and “After double” were tested with the Wilcoxon rank-sum test

Fig. 4 Angle error (from the direction to the nest) before and after reassessment. Circular histogram shows the transport direction (0 is the nest direction). “Before release” represents the indices in the 5 s before the releasing event. “After retouch” represents the indices in the 5 s after the retouching event. “After double” means the indices in the 5 s after the retouching event when another reassessing ant came into contact with the food. The number of replicates of “Before release,” “After retouch,” and “After double” were 68, 68, and 4, respectively. “Before release” and “After retouch” were tested using the Watson–Wheeler test

$W=22.086$, $p<0.001$). There was no correlation between the duration from the releasing event to the retouching event and the distance from the food to the nest at the releasing event (Fig. 5, Kendall’s test; $\tau=0.0038$, $Z=0.049862$, $p=0.9602$).

When an ant individual began pulling the food just after reassessment, we occasionally observed cases where another ant also retouched the food almost at the same time and transported it together with the previously reassessing ant accidentally (Movie S2). To investigate if the efficiency of reassessment increases with the number of reassessing ants, we compared the three indices for assessment behaviors either performed by two reassessing individuals simultaneously or by a single individual. The results showed that there was no statistical difference regardless of the presence or absence of an additional reassessing ant (Fig. 3; Wilcoxon rank-sum test: moving distance, $W=103$, $p=0.2843$; straightness, $W=141$, $p=0.8167$; Fig. 4; sample size is not sufficient for performing Watson–Wheeler test correctly).

From these results, we conclude that the reassessment occurred in the following order of events: (1) the speed to the nest decreases; (2) the individual pulling the transport leaves the food item; (3) she explores the area surrounding the food and finds the right path to the nest; (4) she returns to the food; and (5) she pulls the food toward the nest again, more accurately than before the reassessment.

Fig. 5 Duration between the releasing event and the retouching event. **a** Histogram of the duration between the releasing event and the retouching event (20.8 ± 20.7 s; mean $\pm$ SD). **b** Relationship between the distance from the nest at the releasing event and the duration of reassessment

Reassessment was responsible for increasing the approach speed depending on the number of transporters

Previously, we described that the LMM test showed that the approach speed increased with the transporter number (number of transporters) in colony A (Fig. 1b, Table. 2). However, this result does not necessarily mean that an increase in transporter number increased the transport accuracy, because reassessment would potentially increase the speed depending on the transporter number (see ESM Simulation). We counted the actual transporter number, excluding reassessing ants from the experimental data after the retouching event (Fig. S4), and analyzed it using LMM (see “Materials and methods”). Having eliminated the effect of reassessment, the transport and approach speed did not change depending on the transporter number (Tables 3, 4; Fig. 6). These results suggest that the increase in approach speed with an increase in the transporter number observed in colony A was presumably because of the effect of reassessment.

Discussion

In this study, we revealed some behavioral features of uncoordinated cooperative transport in *F. japonica*. First, it was not evidence that the approach and instantaneous transport speeds increased with the transporter number (number of transporters) in our experiment. Second, route reassessment behavior improves the accuracy and efficiency of transport. These observations suggest that a single *F. japonica* ant plays an outstanding role in a cooperative transport trial, regardless of the number of transporters attached to the food item. It remains to be determined if this role is fixed to specific individuals, or alternates among individuals over time; this should be examined by long-term monitoring, with the tracking of individual behavior.

We revealed how *F. japonica* renews its route information during transport by performing a series of behaviors that was herein named reassessment. One reassessment

Table 3 Summary of the linear generalized mixed effect model (LMM) in instantaneous transport speed without reassessing ants

Fixed effect						Random effect	
Parameter	Estimate	SE	df	t value	p value	Parameter	SD
Intercept ^a	1.0945	0.09744	99.85546	11.233	0.00125	Residual	0.3566
Transporter number	0.02974	0.01874	219.7031	1.587	0.114	Trial	0.2215
Colony ^b	−0.20499	0.13083	85.59356	−1.567	0.121		
Transporter number $\times$ colony ^c	−0.02901	0.02121	218.12392	−1.368	0.173		

Instantaneous transport speed depending on the transporter number and colony without reassessing ants

^aIntercept of regression line

^bCategorical fixed effect. In colony A, colony = 0; in colony B, colony = 1

^cInteraction term

Table 4 Summary of the linear generalized mixed effect model (LMM) approach speed without reassessing ants

Fixed effect						Random effect	
Parameter	Estimate	SE	df	t value	p value	Parameter	SD
Intercept ^a	0.50250	0.1067	130.9	4.708	<0.001	Residual	0.4364
Transporter number	−0.00013	0.0225	224.7	−0.006	0.99500	Trial	0.1811
Colony ^b	−0.11460	0.1415	111.1	−0.810	0.42000		
Transporter number × Colony ^c	−0.02317	0.0255	223.6	−0.909	0.36500		

Approach speed depending on the transporter number and colony without reassessing ants

^aIntercept of regression line

^bCategorical fixed effect. In colony A, colony = 0; in colony B, colony = 1

^cInteraction term

Fig. 6 Approach and instantaneous transport speeds with different numbers of transporters without reassessment ants. **a** Approach speed with different numbers of transporters. **b** Instantaneous transport speed with different numbers of transporters. The plot represents the median value of speed in a trial. The numbers of replicates were $n=23, 27, 30, 28, 27, 24, 19, 19, 13, 8, 6, 4, 2$, and 2 for experiments with transporter numbers of 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, and 14, respectively. Red bars show the standard deviation and red rhombuses represent the means of the median speed values

was observed under transient individual transport during cooperative transport. We showed that not only the direction to the goal, which had been analyzed by previous studies (Schwarz et al. 2017), but the straightness and moving distance of transport, were improved by reassessment. These results suggest that reassessment improves cooperative transport and leads to successful transport. It should be noted that this behavior should appear to be causing a deadlock, because the transport speed decrease considerably during the time that the reassessing ant is away from the food. Retrospectively, the relatively shorter duration of ants' contact with food in uncoordinated cooperative

transport in *F. pallidefulva*, *F. obscuripes*, and *F. podzolica* (McCreery 2017) could be due to reassessment-like behavior. The duration that reassessing ants are away from a food item in *F. japonica* (several tens of seconds) was longer than that for peeking in *C. velox* (several seconds) (Schwarz et al. 2017). This difference would be primarily due to a species-specific behavioral difference or a difference in experimental conditions. In this study, ants were allowed to use only limited visual cues, i.e., fluorescent light and the nest. In addition to this information, *F. japonica* might use hydrocarbon gradients near the nest as a cue (Sturgis et al. 2011). A previous study of *C. velox* allowed

ants to use the celestial compass and landmarks under field conditions (Schwarz et al. 2017). However, *C. velox* did not see the nest directly and did not use hydrocarbon gradients near the nest under their experimental conditions. Moreover, the distance from the nest to the food in our experiments was shorter (~0.3 m) than that in the experiments by Schwarz et al. (2017) (several meters). It would be interesting if the transient departure from the food during backward-walking, including peeking, foodless search loop, and reassessment, is a general strategy to update map information regardless of the available cue types.

In cooperative transport, the role of newly attached ants with route information (as mentioned in the “Introduction”) in *P. longicornis* (Gelblum et al. 2015) and reassessing ants in *F. japonica* are similar, in that a single ant controls the movement of the group. However, it is reported that *P. longicornis* is additionally guided by pheromones during its cooperative transport (Fonio et al. 2016). Thus, a difference between cooperative transport without deadlock in *P. longicornis* and that with deadlock in *F. japonica* would possibly be because of the availability of pheromones.

If only the reassessing ant can control or improve uncoordinated cooperative transport in *F. japonica*, the ecological relevance of increasing the number of transporters in this type of cooperative transport is unknown. It is possible that transporters are involved in recruitment and/or defense behavior(s). Recruitment is a general behavior in cooperative retrieval (not only cooperative transport) (Hölldobler and Wilson 1990). Defense against competitors for live prey may be the most important role (Czaczkes et al. 2013; Traniello and Beshers 1991). In *F. pallidiflava*, the ability to secure a food item from competitor species increases with an increase number of transporters (Traniello and Beshers 1991). In *P. longicornis*, some ants follow the carried item without assisting in cooperative transport; these are called “escorts.” Escorts prevent a living prey from escaping (Czaczkes et al. 2013). In *F. japonica*, during reassessment, it may be necessary for other ants to defend the food item.

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Compliance with ethical standards

Conflict of interest There are no conflicts of interest to declare.

Ethical statement All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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