

RESEARCH ARTICLE

Collective strategy for obstacle navigation during cooperative transport by ants

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ABSTRACT

Group cohesion and consensus have primarily been studied in the context of discrete decisions, but some group tasks require making serial decisions that build on one another. We examine such collective problem solving by studying obstacle navigation during cooperative transport in ants. In cooperative transport, ants work together to move a large object back to their nest. We blocked cooperative transport groups of *Paratrechina longicornis* with obstacles of varying complexity, analyzing groups' trajectories to infer what kind of strategy the ants employed. Simple strategies require little information, but more challenging, robust strategies succeed with a wider range of obstacles. We found that transport groups use a stochastic strategy that leads to efficient navigation around simple obstacles, and still succeeds at difficult obstacles. While groups navigating obstacles preferentially move directly toward the nest, they change their behavior over time; the longer the ants are obstructed, the more likely they are to move away from the nest. This increases the chance of finding a path around the obstacle. Groups rapidly changed directions and rarely stalled during navigation, indicating that these ants maintain consensus even when the nest direction is blocked. Although some decisions were aided by the arrival of new ants, at many key points, direction changes were initiated within the group, with no apparent external cause. This ant species is highly effective at navigating complex environments, and implements a flexible strategy that works for both simple and more complex obstacles.

KEY WORDS: Self-organization, Emergent phenomena, Formicidae, Problem solving, Decentralized coordination, Swarm intelligence

INTRODUCTION

From multi-cellular organization to massive animal migrations, emergent group behaviors are ubiquitous and drive much of the complexity of the biological world. Tasks are often accomplished without a leader (Camazine et al., 2001), as impressive group behavior emerges from individual-level interactions. Ant colonies are model systems for studying emergent group behavior because of the complexity and scale of the tasks they cooperatively accomplish. A crucial task for many animal groups, including ants, is making collective decisions, and a substantial body of studies deals with how groups accomplish this with discrete, single-step decisions (Conradt and Roper, 2005; Deneubourg and Goss, 1989; Sumpter

and Pratt, 2009), such as nest site selection in honey bees or *Temnothorax* ants (Pratt, 2005; Pratt et al., 2002; Seeley, 2010). In contrast, we know less about how groups collectively accomplish complex tasks that require a series of decisions, each building on previous ones. This type of behavior is akin to problem solving, and has been studied primarily in individuals rather than groups. For example, maze-solving has been studied in many taxa including rats (Mulder et al., 2004; Yoder et al., 2011) and single-celled slime molds (Nakagaki et al., 2000; Reid and Beekman, 2013; Reid et al., 2012). Groups making serial decisions face the additional challenge of maintaining consensus – defined as agreeing on a single option (Sumpter and Pratt, 2009). In this study, we examined collective problem solving by coordinated groups of ants in a task similar to a maze.

A conspicuous example of collective behavior in ants is cooperative transport, in which ants work together to move a large object, intact, back to their nest (reviewed in Berman et al., 2011; Czaczkes and Ratnieks, 2013; McCreery and Breed, 2014). Cooperative transport is challenging because it requires moving an object over heterogeneous terrain while maintaining consensus about travel direction. Ants can generally sense the direction of their nest (e.g. Cheng et al., 2014; Steck, 2012; Wehner, 2003) and in many cases groups can form consensus to move toward their nest (Berman et al., 2011; Czaczkes et al., 2011; Gelblum et al., 2015). However, if the nest direction is blocked by an unexpected obstacle, the situation is substantially more challenging. The group's shared homeward bias is no longer helpful. In order to proceed, the group must find a consensus on a new travel direction and navigate around the obstacle, continuously updating the direction until it is possible to resume unobstructed movement toward the nest.

How a group solves this problem – their 'strategy' – impacts the kinds of obstacles they can successfully navigate. Consider a simple strategy: when a transport group encounters an obstacle, they choose a direction to move around the obstacle perimeter until they can again move, unobstructed, toward the nest. This strategy requires information about nest direction and the ability to form consensus on travel direction, both of which are plausible for groups of ants. However, this simple strategy only works with simple obstacles; groups using this strategy would get stuck in a concave obstacle, which would require moving away from the nest to succeed. Navigation strategies exist that would be successful for any possible obstacle, but require more information (e.g. Table 1) (Kamon and Rivlin, 1997; Murphy, 2000). We define these strategies as 'robust' because they are successful over a range of obstacle shapes. But robustness comes at a cost in terms of energy and information processing. Thus, there is a trade-off between simple strategies that are easy for groups to execute but may fail, and strategies that are robust with respect to obstacle shapes, but more costly.

We investigate obstacle navigation during cooperative transport in *Paratrechina longicornis* (Latreille 1802), the longhorn crazy ant.

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Table 1. Predictions for efficiency of navigation in the wall and the cul-de-sac with example strategies of different robustness

Example strategy	Description	Prediction
None	Groups move in the direction of the nest; however, when that direction is obstructed they are unable to form consensus on a new direction.	Groups fail to navigate any of the obstacles.
Simple 1	Groups move in the direction of the nest whenever possible. If obstructed, the group can form consensus on a new direction, and they follow the obstacle perimeter until the nest direction is available. This requires the ability to estimate nest direction and to form consensus on a travel direction even when the nest direction is unavailable.	Groups succeed at navigating the wall but fail to navigate the cul-de-sac, because in the cul-de-sac the nest direction becomes available before navigation is complete. This strategy fails on all non-convex obstacles (Lumelsky and Stepanov, 1987).
Extremely robust 1	Groups move towards nest direction whenever possible; if obstructed, groups move around obstacle as in the 'simple 1' strategy. However, the group only leaves the obstacle perimeter when the nest direction is available and the nest is closer than at any other point during navigation. This strategy requires the ability to estimate distance to the nest.	Groups will successfully navigate both the wall and the cul-de-sac with maximum efficiency (sinuosity=1 for each). This strategy is known to solve arbitrarily complex obstacles (Kamon and Rivlin, 1997). Multiple strategies exist that are extremely robust, but all require more information processing than the 'simple 1' strategy.
Extremely robust 2	Groups follow the 'extremely robust 1' strategy described above, but if they navigate over ground they have already moved over, they abandon the transport effort. This requires detecting when they move over their footsteps, which can be accomplished through path integration, for example.	Groups will successfully navigate both the wall and the cul-de-sac with sinuosity=1 for each. This strategy also succeeds in the trap because individuals can give up, moving on to other useful behaviors.
Intermediate strategies	There are many possible strategies that would lead to moderately robust navigation. All require more information than the simplest strategy. Using trajectory data, we can infer properties of the strategy.	Groups succeed at both the wall and the cul-de-sac. Efficiency for the wall may be higher (lower sinuosity) than for the cul-de-sac. Efficiency is lower than an extremely robust strategy (sinuosity>1) for both obstacles.

Workers of this species are known to be excellent transporters (Czaczkes et al., 2013; Gelblum et al., 2015). *Paratrechina longicornis* is in the subfamily Formicinae and is a widely distributed 'tramp' ant (Wetterer, 2008). We presented groups of ants with obstacles of varying difficulty in order to investigate the navigation strategy they use, and where their strategy falls between simple and robust problem solving. We obstructed ant cooperative transport groups with three increasingly complex obstacles: an obstacle that simple strategies can easily navigate (the 'wall'), an obstacle that requires a more robust strategy (the 'cul-de-sac') and an impossible obstacle that thwarts even robust strategies (the 'trap') (Fig. 1). Example strategies with their predictions are shown in Table 1. Our main questions were: (1) how robust is the strategy of groups of ants; (2) what strategy do the ants use; (3) how do individuals contribute to the group's strategy; and (4) when facing an obstacle that is impossible to navigate, do groups have the ability to detect traps, and if so, what is their response?

MATERIALS AND METHODS

Overview

We gave ants foraging near a colony entrance pieces of tuna to carry. After a group of ants had begun carrying the tuna, and their preferred direction of travel was established, we put one of three obstacles in their path, directly blocking that preferred direction. We video recorded these trials and extracted data from the videos, including the trajectory of the piece of tuna, which we used to measure additional results metrics, described below.

For question 1, we examined strategy robustness by looking at which obstacles groups of ants could navigate, their efficiency at the wall and the cul-de-sac, and how well they maintained consensus about travel direction (Table 1). For question 2, we identified behavioral elements (e.g. perimeter following) that make up the strategy. For question 3, we examined individual behaviors during key decisions in obstacle navigation, to look for precipitating events such as ants joining. For question 4, we compared group behavior in the cul-de-sac and the trap.

Study sites

We conducted fieldwork in June 2014 at two sites: Arizona State University in Tempe, Arizona, and the Biosphere 2 facility in Oracle, Arizona, using two colonies in Tempe and two at Biosphere 2 (four colonies total). We worked in locations having a flat surface, with relatively constant shade, and close to only one nest entrance so that all foragers had the same goal. The general pattern of navigation behavior, including strategy, was similar among these four colonies.

Obstacles and strategy

We used three types of obstacles. (1) The simplest obstacle (Fig. 1A), hereafter referred to as the 'wall', requires a form of symmetry breaking: groups must choose a direction from equal options. We placed obstacles approximately perpendicular to groups' travel direction, blocking the nest direction. Two of the remaining options (left and right) are of equal value, so a choice between them requires breaking symmetry. (2) A complex obstacle (Fig. 1B), the 'cul-de-sac', also requires breaking symmetry, but has an additional challenge. Groups navigating this obstacle must move opposite to their preferred direction (away from the nest) to succeed. The last obstacle (Fig. 1C), the 'trap', resembles the cul-de-sac but is impossible to navigate. However, there are strategies that would allow groups to know that they are trapped. In natural settings, such strategies are more robust, because if groups recognize that navigation has failed, individual ants can abandon the transport and switch to other behaviors. For example, without their load, ants may be able to escape and return to the nest.

Navigation strategies are also of interest in robot navigation, and a substantial body of literature predicts the consequences of various navigation strategies in the presence of obstacles of varying complexity (Kamon and Rivlin, 1997; Lumelsky and Stepanov, 1987; Murphy, 2000). Although we do not expect ants to use any specific strategy from this literature, we used these predictions to design our obstacles, so that we know a strategy that can solve each one. We compared the ant groups' trajectories to the predictions for these theoretical strategies, listed in Table 1. Groups without a navigation strategy fail to reach consensus if obstructed. In the 'simple 1' strategy, groups

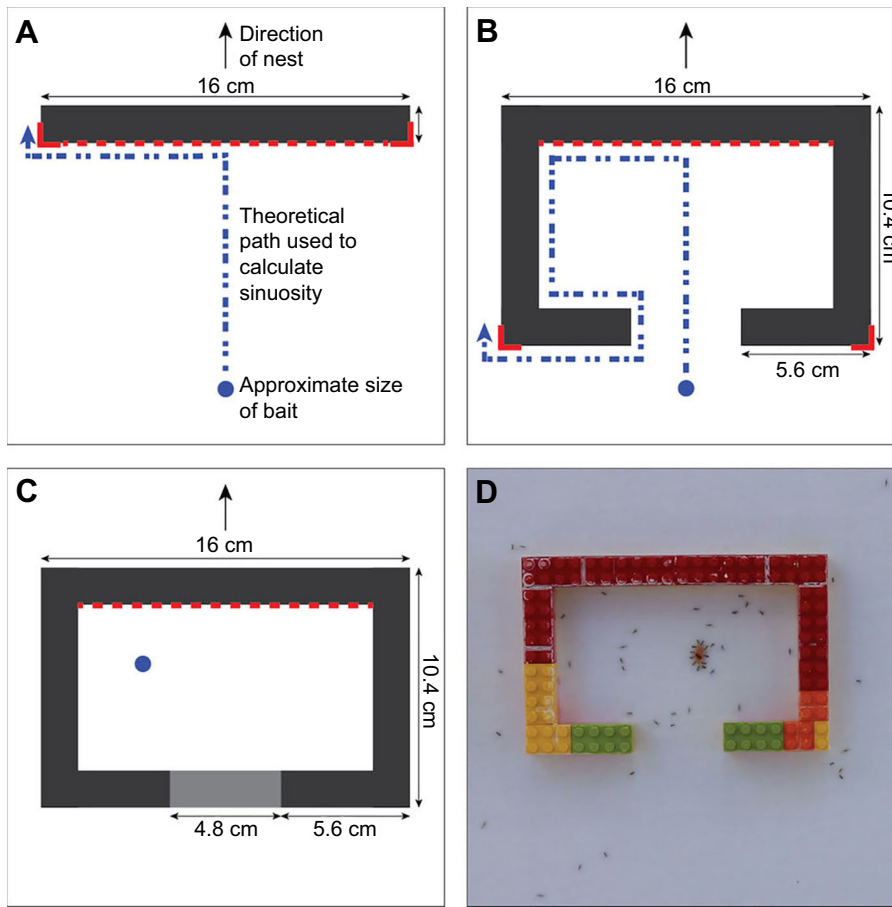


Fig. 1. Shapes and dimensions of obstacles used to block cooperative transport groups. (A) The wall; (B) the cul-de-sac; and (C) the trap. Red dashed line indicates the 'back wall' as referenced in the text. We defined obstacle navigation as beginning when the group reached this back wall, and ending when the group had rounded one of the corners marked in red. The blue dashed line indicates the theoretical 'shortest' path used to calculate sinuosity, and the blue circle indicates the approximate size of the bait. (D) An example of a trial with the cul-de-sac.

follow the perimeter of an obstacle and move toward the nest if possible. This strategy succeeds at the wall, but fails at the cul-de-sac. Groups using the 'extremely robust 1' strategy follow the perimeter of an obstacle until they can move toward the nest, and they are also closer to the nest than they have been previously. This strategy is efficient for both the wall and the cul-de-sac, but groups using this strategy in the trap will continue attempting to navigate it indefinitely. In the 'extremely robust 2' strategy, groups use the same rules as the 'extremely robust 1' strategy, but additionally they abandon navigation if they travel where they have already been. This allows groups to detect that they are trapped. Strategies that succeed with a wider range of obstacle types require more information processing than simpler strategies (Table 1). The strategies included here are just examples; the range of potential strategies is large, and strategies could include more stochasticity. For example, groups may follow the perimeter of an obstacle until the nest direction is available, at which point they move toward the nest with some probability, otherwise continuing to follow the perimeter. Stochastic strategies may allow groups to navigate a wider range of obstacles, but their efficiency with a given obstacle will be different in each encounter.

All potential strategies are composed of behavioral elements. Examples of elements included in the strategies in Table 1 are perimeter following, moving toward the nest, moving away from the nest and remembering the path traveled. Other possible elements include spontaneous direction changes and random walks.

Experiment details

At the beginning of each trial, a fresh piece of 11×17 inch (28×43 cm) white paper was placed on a flat surface near a nest entrance. We set up

in locations where all successful foragers returned to the same entrance, to ensure that individuals in our transport groups would have the same goal. The nest entrance was at least 15 cm away from our experiment. At the start of each trial, a dead cricket was placed on the paper, so that foragers would recruit by laying pheromone. We used a cricket to elicit a strong recruitment response, so that transports would not be limited by insufficient workers. When a group of workers began moving the cricket, we replaced it with a marked piece of tuna, lighter than the cricket (0.031–0.105 g). Once a group of workers had moved the tuna at least 10 cm, one of the obstacles was placed in their path, oriented such that the 'back wall' (dashed red line in Fig. 1) was perpendicular to their preferred direction. For the trap, we first obstructed their path with an obstacle shaped like the cul-de-sac. After the group entered this obstacle, we placed a 'door' in the exit to trap groups. We ended trap trials after 12 min; this was more than sufficient to capture group behavior. We did not try to eliminate additional ants from being in the vicinity of the transport effort. These 'extra' ants, also known as escorts, are common in natural *P. longicornis* transport efforts (Czaczkes et al., 2013), and whatever effect they have on navigation would also be present in natural navigation efforts.

These escort ants did not alter pheromone trails to help groups navigate around obstacles. *Paratrechina longicornis* workers lay a specialized pheromone trail to recruit ants to a large item, but cooperative transport groups do not use that trail to navigate back to the nest (Gelblum et al., 2015). The recruitment trail is short-lived, decaying within 6 min (Czaczkes et al., 2013), and workers laying this trail have a conspicuous, halting movement pattern that we did not observe during navigation. Instead of relying on a pheromone trail, recent studies suggest that transport groups in *P. longicornis* can be

aided in returning to the nest by new ants joining the effort (Gelblum et al., 2015). To rule out the possibility that other workers provide another type of global directional cue, we conducted an experiment to see how long an obstacle must be in place before ants avoid it altogether. In our experiment, the vast majority of ants moving from sugar-water baits toward a nest initially hit the obstacle we placed in their path, but eventually ants' paths changed so that they avoided the obstacle. However, this change took over 20 min, while our longest trial was only 10.8 min (Fig. S1). Over the length of time that our trials lasted, ants' paths had not substantially changed to avoid obstacles. Escort ants may yet provide cues to cooperative transport groups through physical contact or another mechanism, but it is unlikely that they provide global cues conveying directional information.

All trials were recorded using a Canon Rebel T2i with lens EF-S 18-55IS (1920×1080, 30 frames s⁻¹; Canon, Tokyo, Japan). All obstacles were constructed out of Lego (Billund, Denmark) and coated on the inside with Insect-a-Slip (Fluon, BioQuip, Gardena, CA, USA) to prevent groups climbing over them.

A total of 91 trials were conducted. However, we excluded trials in which the following occurred: (1) foragers recruited from multiple nest entrances, (2) the tuna piece was light enough to be moved substantial distances by a single ant or (3) the group first encountered the obstacle by hitting more than 3.2 cm from the center of the back wall (to ensure that groups would be forced to choose a direction from among relatively equal options). After excluding these trials, we were left with a total of 61 trials: 22 for the wall, 19 for the cul-de-sac and 20 for the trap.

Data extraction

Several types of data were extracted from each of these 61 videos. We manually recorded the location and orientation of the tuna piece every second using MATLAB (The MathWorks, Natick, MA, USA). This provides the trajectory of the group rather than of individual ants. The location of the obstacle was also recorded for each trial. We used this trajectory information to measure speed, sinuosity and backward runs, and to identify the sharpest turns in the wall and escape points in the cul-de-sac, as described below.

Speed

We used speed to evaluate how well groups maintain consensus (for question 1) and to compare group behavior in the cul-de-sac and the trap (question 4). Because group size and speed were correlated (see Results), we also used speed to evaluate how individuals affect efficiency (question 3). Speed was measured every second, so it approximates instantaneous speed. When the speed was extremely low (less than 0.048 cm s⁻¹), we classified the group as being 'stalled'. For analyses in which we compared speeds across trials, we eliminated speed data for times until the group first reached a threshold speed of 0.24 cm s⁻¹.

Sinuosity

Sinuosity is defined as the ratio of the path length to length of the shortest path. Paths with lower sinuosity are more efficient. We used sinuosity to compare navigation efficiency among obstacles (question 1). Here, in order to directly compare obstacles, we used a modified measure of sinuosity: the path length divided by the path that would be taken if groups followed the perimeter of the obstacle (Fig. 1A,B).

Backward runs

For the cul-de-sac, successful navigation requires moving away from the nest. We evaluated the extent to which groups did this by

quantifying the number and distance of 'backward runs'. A backward run is a period of time during which the group is moving away from the nest (and away from the back wall). Backward runs occur when the distance from the tuna to the back wall is increasing, and the run ends when this distance decreases. For each backward run, we recorded the time at which the run started, and the displacement away from the back wall that occurred during that run. Analyzing backward runs provided insight into strategy elements (question 2) and we also compared backward runs in the cul-de-sac and the trap (question 4).

Sharp turns

Transport groups sometimes turn sharply during navigation. In these instances, the consensus travel direction changes. We carefully examined these sharp turns to determine what may have caused these changes in consensus, with particular emphasis on whether individual ants seemed to cause the change (question 3). To simplify our analysis, we only examined turns occurring while groups navigated the wall. For each trial, we calculated a turning angle every second by taking the mean direction over the three previous seconds and over the three subsequent seconds. We carefully examined every point that had a turning angle equal to or greater than 2.5 rad (~145 deg). We chose 2.5 rad because it resulted in 38 unique turns for all the wall trials, which was a reasonable number to carefully examine manually. Each of these turns was placed into one of four categories based on what may have caused it: (1) a new ant joined the transport effort, (2) an ant left the transport effort, (3) the group hit the obstacle or (4) there was no discernible cause (i.e. none of the above). We used a similar method to find the number of turns greater than 90 deg for all obstacles, to examine how group size affects number of turns (question 3).

Escape points

Escape points are turns that led to successful completion of the navigation. We examined escape points in the cul-de-sac to evaluate how individual ants contributed to escape (question 3). We define the escape point of each trial as the last turn the group made, such that after making the turn they left the interior of the cul-de-sac, while before making the turn they would not have done so. We manually identified each escape point from images of the trajectories; our designation of escape points was therefore blind with respect to the behavior of individuals. We placed each escape point into one of the same four categories listed for sharp turns.

In addition to these results metrics that we measured from group trajectories, we manually measured navigation time (for question 1) and group size (for question 3). For navigation time, we defined the start of navigation as when a group first appeared to respond to the 'back wall', and we defined the end of navigation as when they rounded one of the bottom corners (colored in solid red in Fig. 1). To find group size, we counted the number of ants attached to the tuna every 15 s.

Statistical analysis

All statistical analyses were performed in R version 3.2.2 (R Foundation for Statistical Computing, Vienna, Austria).

Question 1: How robust is the navigation strategy of groups of ants?

We compared efficiency data in the wall and the cul-de-sac with a *t*-test on sinuosities; data were log-transformed to meet assumptions of normality. To examine how well groups maintain consensus, we compared stalls and speeds while groups were navigating and while unobstructed. The proportion of time groups were stalled was

analyzed with a Bayesian zero-inflated beta model using Stan implemented in R (<http://mc-stan.org>). We chose this method because these data were heavily zero-inflated, such that general or generalized linear models were inappropriate. We used a binomial model to examine the probability of never stalling, and for trials with at least one stall, we used a beta model to look at the proportion of time stalled. We evaluated the effect of potential predictors on this proportion, but not on the probability of never stalling, because this probability is biased among obstacles: groups are less likely to never stall in the cul-de-sac because it takes them longer to navigate it. Priors were relatively vague and did not substantially impact posteriors.

We used general linear models to analyze square-root transformed speeds using the lme4 package (Bates et al., 2015). Transformed speeds were normally distributed. As potential predictor variables, we included whether the group was navigating an obstacle or unobstructed, and which obstacle was navigated. We compared a full model with both predictors and their interaction with simpler models with one or both predictors without the interaction (Table S1). We also included random effects of trial nested within colony. We compared models with Akaike's

information criterion (AIC) to determine the best predictor variable(s).

Question 2: What strategy do groups use?

We qualitatively examined trajectories to identify strategy elements. To examine how backward movements contribute to strategy, we analyzed distances of backward runs in a Bayesian framework using JAGS in R (version 3). We saw how behavior changed over time by modeling the distribution of backward run distances as a gamma distribution, where the shape parameter, k , can change in time according to the following equation:

$$k = e^{\alpha_i + \beta t}, \quad (1)$$

where α_i represents a random intercept for each trial and β indicates the extent to which k changes over time (t). Gamma distributions with larger shape parameters are more right-skewed. We also fit additional parameters indicating the scale of the gamma distribution and the mean and standard deviation of α_i . We verified this model by simulating hundreds of data sets and checking that the 95% credible interval (CI) included the true parameter 95% of the time. We examined whether the distribution of backward run distances changes over time by evaluating whether β is different from zero. Our priors did not substantially impact posteriors. To avoid bias in the timing of large backward runs, we excluded any backward run that led to the group completing obstacle navigation.

Question 3: How do individuals contribute to the group's strategy?

In addition to a qualitative analysis of sharp turns and escape points, we examined the effects of group size and speed on performance using Pearson product-moment correlations, with log-transformed data where necessary. We also examined the effect of group size on speed and on the number of turns using Kendall rank correlations, as speed data and number of turns in each trial could not be transformed appropriately for a Pearson correlation because of non-normality. These analyses allow us to see how individuals affect efficiency through group size.

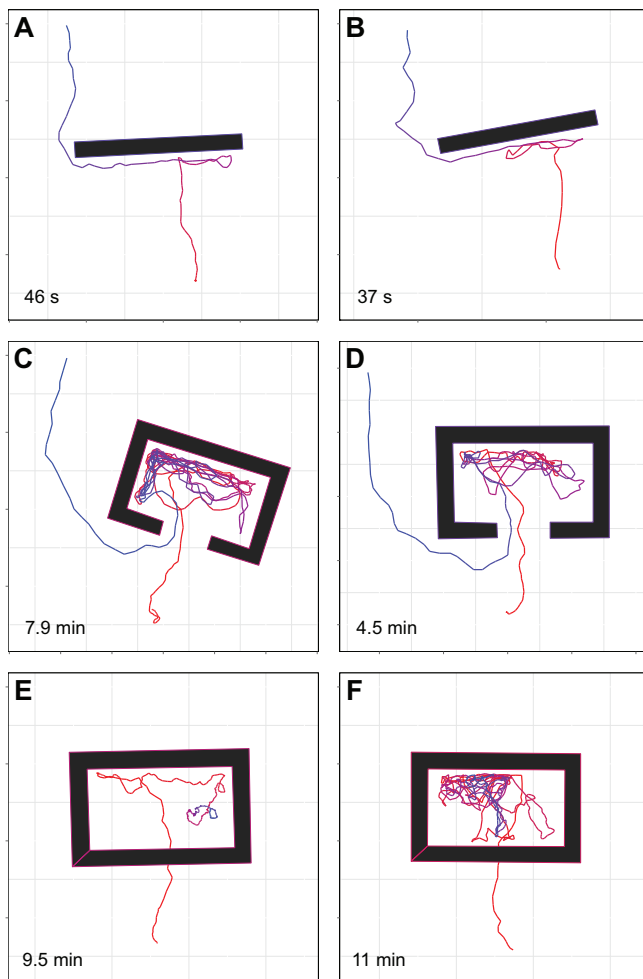


Fig. 2. Examples of group trajectories. Warmer colors indicate early points in the navigation process, while cooler colors are later in time. (A,B) The wall; (C,D) the cul-de-sac; (E,F) the trap. Times shown in the bottom left corner of each panel indicate the time it took to navigate the obstacle (from hitting the back wall to rounding the corner) for A–D, and the time spent trapped for E and F.

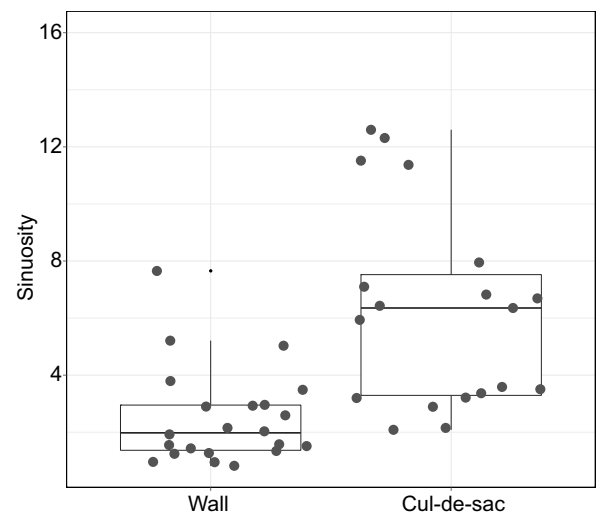


Fig. 3. Efficiency (sinuosity) of cooperative transport for groups navigating the wall ($n=22$) and cul-de-sac ($n=19$). Large circles show jittered sinuosity values for each trial. Groups navigating the wall and the cul-de-sac had significantly different sinuosities (unpaired t -test, $t_{30}=5.05$, $P<0.0001$). Boxes include 50% of the data (25th to 75th percentiles), and whiskers extend to the lowest and highest values that are within 150% of the interquartile range. The small circle is a point outside that range.

Table 2. Proportion of time spent stalled while unobstructed (before or after obstacle navigation) and during obstacle navigation

Obstacle	Mean proportion of time stalled	
	While unobstructed	While navigating obstacle
Wall ($n=22$)	0.014 (0.0086)	0.016 (0.0076)
Cul-de-sac ($n=19$)	0.017 (0.0063)	0.016 (0.0037)
Trap ($n=20$)	0.014 (0.0080)	0.24 (0.034)

Values shown are means of these proportions for each trial, including trials with zero stalls. Standard errors are shown in parentheses.

Question 4: How do groups behave with an impossible obstacle?

To determine how group behavior differs in the trap and the cul-de-sac, we qualitatively analyzed speed and group size over time in these obstacles. We used the *ggplot2* package (Wickham, 2009) to visually compare these metrics, smoothing the speed data with local regression (LOESS) or generalized additive models (GAM), depending on the number of observations. We also compared stalls and backward runs in the cul-de-sac and the trap, using statistical tests described above.

RESULTS

How robust is the navigation strategy of groups of ants?

Paratrechina longicornis groups successfully navigated both the wall ($n=22$) and the cul-de-sac ($n=19$) in every trial. Examples of groups' trajectories are shown in Fig. 2 (Figs S2–4 show group trajectories for all trials; Movie 1 shows the complete navigation for Fig. 2A,C). The mean (\pm s.e.m.) times to navigate the obstacles were 1.01 ± 0.17 min for the wall and 5.99 ± 0.52 min for the cul-de-sac, with a mean speed across trials of 0.43 cm s^{-1} . Although groups always solved both obstacles, they were significantly more efficient solving the wall than the cul-de-sac (untransformed sinuosity means \pm s.e.m. = 2.5 ± 0.36 and 6.3 ± 0.80 ; unpaired t -test, $t_{39}=5.05$, $P<0.0001$; Fig. 3).

We also examined how well groups maintain consensus. We expected groups lacking consensus to stall. Transport groups rarely stalled (<2% of the time) either while navigating obstacles or while unobstructed (Table 2). Groups had a 54% chance of never stalling (probability = 0.54, 95% CI = 0.43–0.64). For trials in which at least one stall occurred, groups spent the same proportion of time stalled regardless of whether they were obstructed. Posterior distributions overlapped substantially for unobstructed groups (mean = 0.044, 95% CI = 0.025–0.081), groups navigating the wall (mean = 0.044, 95% CI = 0.021–0.084) and groups navigating the cul-de-sac (mean = 0.025, 95%

CI = 0.014–0.052). We estimated random intercepts for each colony, but found that colonies did not differ in proportion of time stalled (Fig. S5). The results show that groups rarely stall, and the proportion of time groups are stalled is not affected by either the wall or the cul-de-sac.

To further examine consensus, we evaluated the effect of obstacles on speed using general linear models. The best model included whether the group was obstructed ($\beta = -0.065$), and did not include whether they were navigating the wall or the cul-de-sac. Detailed results of this best-fit model are included in Table S2. Groups slowed down while navigating obstacles and this effect was not different for different obstacles. However, the effect size was small; all else being equal, groups moved only 0.043 cm s^{-1} slower while navigating obstacles. This is approximately a 10% reduction in speed, and this decrease is much smaller than the overall variation in speeds of groups (Fig. S6).

What strategy do groups use?

We looked at elements – the behavioral components of strategy – to answer this question. The primary challenge in navigating the wall is to break symmetry. We could not ensure perfect symmetry among the options for travel direction (obstacles were not always perfectly perpendicular to preferred direction), but groups did not favor the direction closer to their initial travel direction. Upon hitting the wall, *P. longicornis* groups broke symmetry, choosing a single direction to move around it. They did not, however, stick with that chosen direction for the entire navigation. In 14 out of 22 trials (64%), the group changed direction after the initial choice. The groups also navigated directly up to the wall, and typically remained close to the wall perimeter after choosing a direction (Fig. 2, Fig. S2). There was no visual detection and evasion; transport groups did not avoid any of the obstacles.

The cul-de-sac presents an additional challenge in that groups must move counter to their preferred direction. Initial behaviors of groups in the cul-de-sac were similar to those of groups navigating the wall; transport groups first hit the back wall of the obstacle and quickly picked a direction. Early in the navigation process, groups remained close to the back wall, but they did not typically move along the side walls (Fig. 2). Later in the navigation process, groups moved away from the perimeter into the open area within the cul-de-sac. Our results show that in the cul-de-sac, groups moved further backwards (away from the nest) the longer they had been navigating (Fig. 4). More specifically, the distribution of distances of backward runs becomes more right-skewed (shifted toward longer distances)

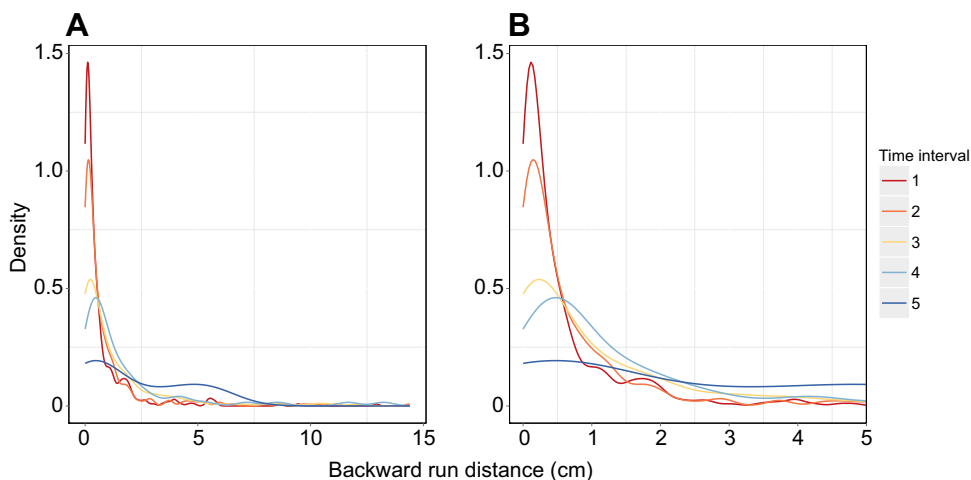


Fig. 4. Densities of backward run distances of groups navigating the cul-de-sac at different time intervals. Each time interval is 134 s long (one-fifth the total time across all trials). (A) All backward run data for the cul-de-sac; (B) same data as in A, but zoomed in to show only backward runs 5 cm or less. Modeled in a Bayesian framework as a gamma distribution with a changing shape parameter, our estimate of the effect of time, β , is 0.13 (95% CI = 0.07–0.20). In the cul-de-sac, the distribution of distances of backward runs becomes more right-skewed over time.

Table 3. *Paratrechina longicornis* strategy elements for obstacle navigation

Element	Description
Move toward goal	If the direction of the goal (nest) is available, move in that direction. <i>Paratrechina longicornis</i> groups especially incorporate this element early in the navigation process.
Symmetry breaking	If encountering an obstacle, choose a direction along the edge of the obstacle to move around it. <i>Paratrechina longicornis</i> broke symmetry when first encountering all three obstacle types.
Perimeter following	Follow the edge of an obstacle while navigating it. <i>Paratrechina longicornis</i> groups followed obstacle perimeters to the left or right, especially early in navigation, but did not typically follow edges that would take them away from their goal.
Spontaneous direction changes	Throughout navigation, incorporate occasional switches in direction (e.g. from moving right to moving left). Such direction changes were present in <i>P. longicornis</i> groups navigating each obstacle, and may prevent extraordinary long navigation times (see Discussion).
Move away from goal ('backwards')	Move away from the goal for brief periods of time. <i>Paratrechina longicornis</i> groups incorporated this element later in the navigation process, increasing the distance of backward movements over time.

over time. Our estimate of β in the cul-de-sac is 0.13, and the 95% CI is 0.07–0.20. We did not find strong evidence for this effect in the wall ($\beta=0.0019$, 95% CI= -0.15 – 0.15 ; Fig. S7A), perhaps because groups navigated the wall rapidly. Transport groups changed their behavior over time. Estimates for all parameters for this analysis are in Table S3. Descriptions of observed strategy elements are included in Table 3.

How do individuals contribute to the group's strategy?

We observed many sharp turns during these experiments, yet stalls were rare. Thus, groups were able to sharply change direction without stalling. We qualitatively examined the sharpest turns made while navigating the wall ($n=38$). In 32% of cases, the change in direction appeared to be caused by a new ant joining the group, in 24% of cases the group hit the obstacle, and in 45% of cases we could see no event precipitating the direction change (Table 4). We conducted a similar analysis of escape points in the cul-de-sac (Table 4). In over half of cases (58%) we could detect no events that seemed to cause the direction changes leading to escape, while 32% were caused by new ants.

In addition to individual contributions at key moments, we examined what effect group size had on transport efficiency. Within the range of group sizes we observed, transport groups with more ants were faster: number of ants and speed were correlated (Kendall's $\tau=0.44$, $P<0.0001$). This correlation was present within colonies as well as in the pooled data (Fig. S8). However, groups navigating the wall with higher average speeds were not more efficient with respect to sinuosity (Pearson's $r=-0.14$, $P=0.53$; Fig. 5A). Furthermore, for the cul-de-sac, faster groups were less efficient, in that they had higher sinuosity (Pearson's $r=0.62$, $P<0.01$; Fig. 5B). This correlation in the cul-de-sac was present across colonies, but not within individual colonies. Colonies at Arizona State University tended to have higher speeds and sinuosities, while colonies at Biosphere 2 tended to have lower speeds and sinuosities (Fig. 5B). Groups with more ants were not more efficient with respect to sinuosity (wall: Pearson's $r=-0.18$,

$P=0.43$, cul-de-sac: Pearson's $r=0.25$, $P=0.30$; Fig. S9A,B), and did not change directions more frequently than smaller groups (wall: Kendall's $\tau=-0.19$, $P=0.25$, cul-de-sac: Kendall's $\tau=0.17$, $P=0.36$; Fig. S9C,D).

How do groups behave with an impossible obstacle?

Groups in the trap behaved starkly differently from groups in the cul-de-sac, across multiple results metrics. We expected groups to behave similarly in the trap and the cul-de-sac, at least initially; however, groups' speeds in these obstacles differ even early in the navigation process, with groups in the trap slowing down dramatically (Fig. 6). This drop in speed corresponds to a reduction in group size (Fig. S10), and an order-of-magnitude increase in the amount of time groups are stalled (Table 2). Furthermore, although our analysis of backward runs indicates that groups have longer backward runs the longer they have been in the cul-de-sac, we found the opposite pattern for the trap ($\beta=-0.22$, 95% CI= -0.26 to -0.19 ; Fig. S7C). This likely results from groups moving more slowly and less often. In the trap, over time, groups explore the space less and less.

DISCUSSION

We presented *P. longicornis* cooperative transport groups with obstacles that require a series of decisions to navigate (problem solving). From their responses, we infer what kind of strategy they use. We predicted that a simple strategy based on nest direction would fail at the cul-de-sac, while an extremely robust strategy would be maximally efficient (sinuosity=1) for both the wall and the cul-de-sac. Neither of these extreme results occurred. Instead, *P. longicornis* uses a moderately robust strategy. Groups of ants were more efficient – took more direct paths in less time – when navigating the wall than the cul-de-sac (Fig. 3), but groups still always succeeded in solving the cul-de-sac. Furthermore, their strategy was stochastic. Trajectories differed greatly from one trial to the next, and groups did not respond predictably when facing a given set of circumstances. While we do not know exactly how robust their strategy is, we show that it is more robust than one based only on nest direction (e.g. the 'simple 1' strategy). Furthermore, because they are more efficient at the wall than the cul-de-sac, we can rule out the 'extremely robust' example strategies in Table 1. In terms of the trade-off between simple, inexpensive strategies that may fail and robust strategies that require more information, this ant species appears to have a solution that lies in between. They can navigate complex obstacles, but not without some cost in terms of efficiency.

In addition to showing that groups can navigate complex obstacles, we were also able to determine how they succeed. Groups have stochastic behavior that changes over time. Early after encountering an obstacle, groups were unlikely to move substantial

Table 4. Apparent reasons for the sharpest turns during wall navigations ($n=38$), and for the last turn leading to escape from the cul-de-sac ($n=19$)

	Ant joined	Ant left	Hit obstacle	No discernible reason
Sharp turns				
Number (out of 38)	12	0	9	17
Percentage	32	0	24	45
Escape points				
Number (out of 19)	6	2	0	11
Percentage	32	11	0	58

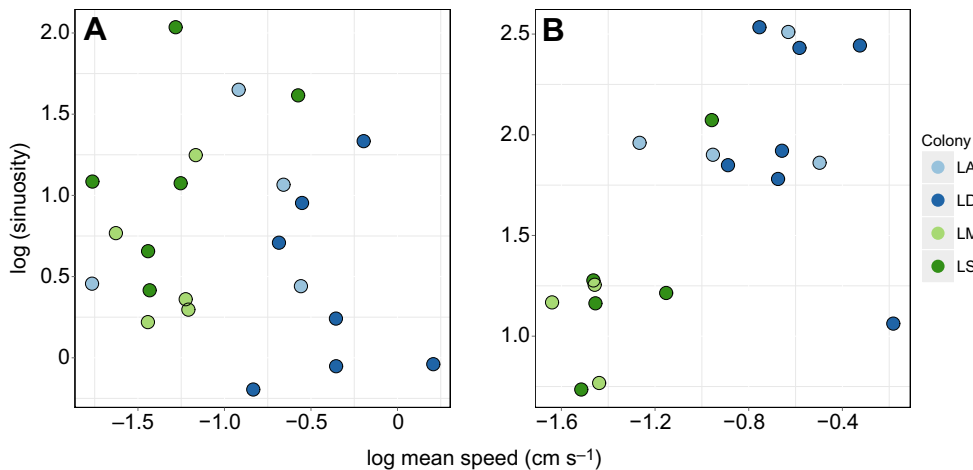


Fig. 5. Relationship between mean speed and sinuosity for groups navigating the wall and the cul-de-sac. Mean speed of groups is not correlated with sinuosity for groups navigating the wall (A; Pearson's $r = -0.14$, $P = 0.53$), and is positively correlated with sinuosity for groups navigating the cul-de-sac (B; Pearson's $r = 0.62$, $P < 0.01$). Blue circles indicate colonies at Arizona State University (light blue: colony LA; dark blue: colony LD) and green circles indicate colonies at Biosphere 2 (light green: colony LM; dark green: colony LS).

distances 'backwards' (away from the nest). This is consistent with groups initially using a simple strategy in which they move in the nest direction whenever possible. This strategy was successful with the wall but not with the cul-de-sac. Groups navigating the cul-de-sac gradually changed their behavior by incorporating longer backward movements, allowing them to find the exit. If groups had incorporated many backward runs from the beginning, it would have taken them longer to navigate the wall. Thus, changing their strategy over time allows them to rapidly solve simple obstacles, while still eventually succeeding at complex ones.

Regardless of the specific obstacle being navigated, groups were highly effective at maintaining consensus while making serial decisions. These groups chose an initial travel direction after encountering the obstacle, and also frequently decided to change direction. They decided to move backwards or they decided to move toward the nest again. When groups changed direction, they did so rapidly, without stalling, as the proportion of time stalled was the same regardless of whether they were obstructed. Stalls were also rare unless the ants were trapped (Table 2), and their speed was only slightly reduced while navigating obstacles. In the absence of obstacles, maintaining consensus is easier because groups simply move toward the nest. We conclude that transport groups are capable of maintaining consensus even when the nest direction is blocked.

How were groups able to maintain consensus, especially while changing direction? In some cases, direction changes that led to

escape seemed to be initiated by new ants joining the transport effort (Table 3). These new ants may have more information about the shape of the obstacle, and will have arrived using a successful path. Compliance is important in consensus decisions, and if groups rapidly conform to a new individual, as Gelblum et al. (2015) reported, they are likely to succeed. Indeed, we found that in 32% of cul-de-sac trials, the initiation of the escape turn coincided with a new ant joining the group. Yet in the remaining trials no new ant was present, and in 58% of cases we could see no cause for the change. For the sharpest turns we again observed that while a substantial portion of turns coincided with new ants joining (32%), in almost half of the cases (45%) we detected no event precipitating the change. Yet these changes occurred rapidly without stalling. We concur with the conclusion of Gelblum et al. (2015) that these groups rapidly conform to newly imposed directions, and we add that, in the case of obstacle navigation, these new directions do not need to come from new group members. Existing group members may also impose new directions. They may do so randomly, although this suggests that larger groups change direction more frequently, which we did not find across the relatively small range of group sizes we observed. Group members may also impose new directions because of new information they have received, perhaps from unladen ants not interacting with the object. A highly conforming group may rapidly change direction based on cues from a single individual, regardless of whether that individual has recently joined the group.

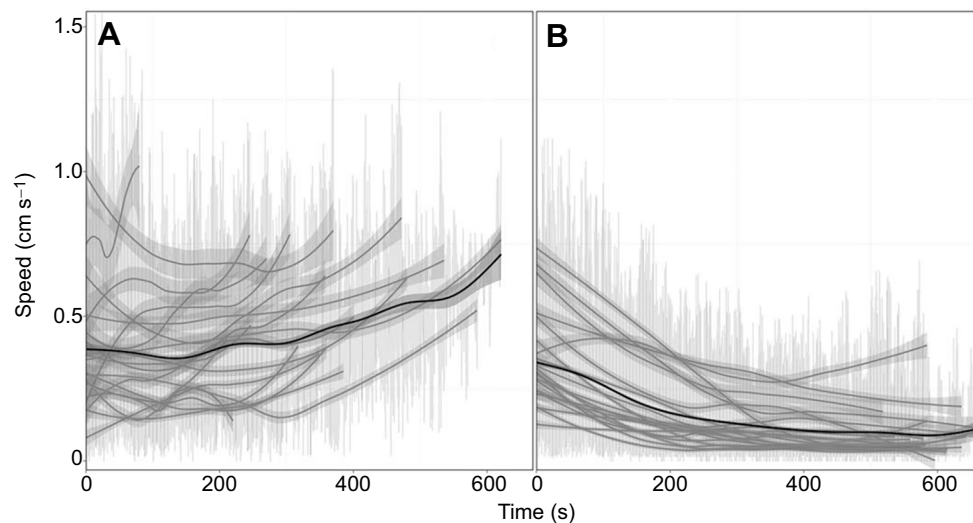


Fig. 6. Speeds of groups over time navigating the cul-de-sac and in the trap. Groups in the trap (B) reduce their speed dramatically, while groups in the cul-de-sac (A) maintain relatively constant speeds. Light grey, unsmoothed lines (background) show raw speed data. Grey, smooth lines show the smoothed speed for each trial, computed with LOESS, and black lines show smoothed speed across trials, computed with GAM.

Groups changed direction frequently, often with no clear external cue for doing so. In some cases these direction changes appeared counter-productive, occurring just before the group would have reached the end of the wall (Fig. 2A,B). Could occasional spontaneous direction changes be beneficial? Assuming groups do not know the shapes of obstacles they navigate, direction changes allow for flexibility and could prevent extraordinarily long navigation times. Consider an obstacle shaped like a very long wall. A group may happen to encounter this obstacle close to the left end, but initially turn right to navigate around it. If they never change direction, they will have to traverse nearly the entire length of the wall. However, if they spontaneously change direction they will find the end relatively quickly. Thus, these spontaneous direction changes allow groups to abandon unsuccessful tactics and try new, potentially fruitful, directions.

In addition to spontaneous direction changes, we observed other strategy elements used by *P. longicornis* (Table 3). Both obstacles require symmetry breaking; after encountering the obstacle, groups must choose a travel direction from equal options. In every trial, groups quickly broke symmetry. Groups also followed the perimeter of the obstacle – with few exceptions groups navigating the wall remained close to the obstacle (Fig. S2). This may simply result from groups being unlikely to move away from the nest. Likewise, groups in the cul-de-sac initially stayed close to the back wall, but typically did not continue following the perimeter to travel ‘backwards’ along the sides of the obstacle. Yet the longer a group was in the cul-de-sac, the more time they spent moving away from the nest. Even then, spontaneous direction changes were always present; direction changes were initially constrained mainly to movement along the back wall, while later, direction changes were less constrained, resulting in a more complete exploration of the space.

These observations give us a partial picture of the group strategy, which initially includes symmetry breaking, moving toward the nest when possible – resulting in perimeter following, and spontaneous direction changes. If the group remains unsuccessful, their behavior changes to include less perimeter following and incorporates a new element: moving ‘backwards’. By investigating how these elements are implemented, future studies could elucidate more about the mechanisms of collective problem solving.

We also investigated the effect of group size on transport and navigation. We found that larger groups moved faster than smaller groups, which agrees with analyses presented by Gelblum et al. (2015). Surprisingly, while larger groups had faster speeds, the increase in speed did not result in faster obstacle navigation. In fact, in the cul-de-sac, faster groups are less efficient. Specific colonies tended to be either relatively slow with low sinuosities or relatively fast with high sinuosities (Fig. 5B).

Although most of our analysis focused on the wall and the cul-de-sac, we also found some unexpected behavior for groups in the trap. The shape of the cul-de-sac and trap only differ by whether there is an exit. We expected trapped groups to behave similarly to groups in the cul-de-sac for at least as long as it took to navigate the cul-de-sac; after this time it is reasonable to imagine that groups may stop trying. Instead, we found that groups have dramatically different behavior in the trap, and the difference is apparent right away. Groups slowed down quickly, and group size decreased as individuals spent less time grasping the object being carried. This suggests that these ants are capable of detecting that they are trapped, or at least detecting a difference in their situation compared with the cul-de-sac.

How do ant groups distinguish between the trap and the cul-de-sac? While the trap keeps the group inside, it also prevents other ants

from entering the obstacle and interacting with the transport group. Perhaps these escort ants are important to the navigation process. Indeed, the presence of nest mates is important in path choices in *Lasius niger*; these ants are more likely to switch paths if they do not encounter nest mates (Czaczkes et al., 2015). Furthermore, escort ants do play an important role when *P. longicornis* groups transport live prey (Czaczkes et al., 2013); perhaps escorts are important even with non-live prey if they must navigate obstacles. Groups may be able to sense how frequently they encounter escorts, and will encounter fewer when trapped. Future work could test this hypothesis by manipulating the number of escorts in trapped and un-trapped conditions, or using a trap from which individuals, but not groups, could enter or escape. Regardless of the mechanism, *P. longicornis* workers have a strategy that is robust in the trap, in that they do not attempt to solve it endlessly.

Overall, our results demonstrate that *P. longicornis* employ a problem-solving strategy that adapts to the complexity of the problem. Future work should aim to understand how this strategy is implemented. How do groups maintain consensus? Perhaps a quorum is required for decisions, as in nest site selection in honey bees and *Temnothorax* (Pratt, 2005; Seeley, 2010), or perhaps informed individuals play an outsized role in decisions (Couzin et al., 2005; Gelblum et al., 2015). How is information integrated and transferred within the group? Information may be transferred through the object itself (Kube and Bonabeau, 2000; McCreery and Breed, 2014), or maybe escorts aid information transfer. This study focused on *P. longicornis*; other species that are effective at cooperative transport, such as *Novomessor cockerelli*, may have evolved completely different strategies. Understanding the range of strategies employed by ant species would lead to new insights into the information processing and collective problem-solving strategies of ants.

Our study also has implications for collective problem solving in other animals. Many animals navigate in groups, from schools of fish to large migrations, and these groups must form consensus to remain cohesive. We show that a group reliant on consensus can collectively make a series of stochastic decisions in order to navigate a complex, unknown environment. In addition, obstacle navigation strategies in *P. longicornis* may provide inspiration for the design of new stochastic strategies for robotics (Bonabeau and Théraulaz, 2000). Ant collective behavior has been a rich source of concepts for research in distributed algorithms, including for cooperative transport by robots (Berman et al., 2011; Rubenstein et al., 2013), and insights from effective social groups such as *P. longicornis* could provide new ideas for designing robot teams that robustly tackle complex environments. Indeed, we show that *P. longicornis* groups are able to collectively navigate complex environments by using a cohesive, flexible and robust navigation strategy.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

H.F.M., R.N., and M.D.B. designed the experiments. H.F.M. and Z.D. conducted fieldwork and contributed to data extraction. H.F.M. and R.N. interpreted data. H.F.M. conducted statistical analyses and wrote the article, with editing contributed from all authors.

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Data availability

Group trajectories and associated files are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.7j2t2>.

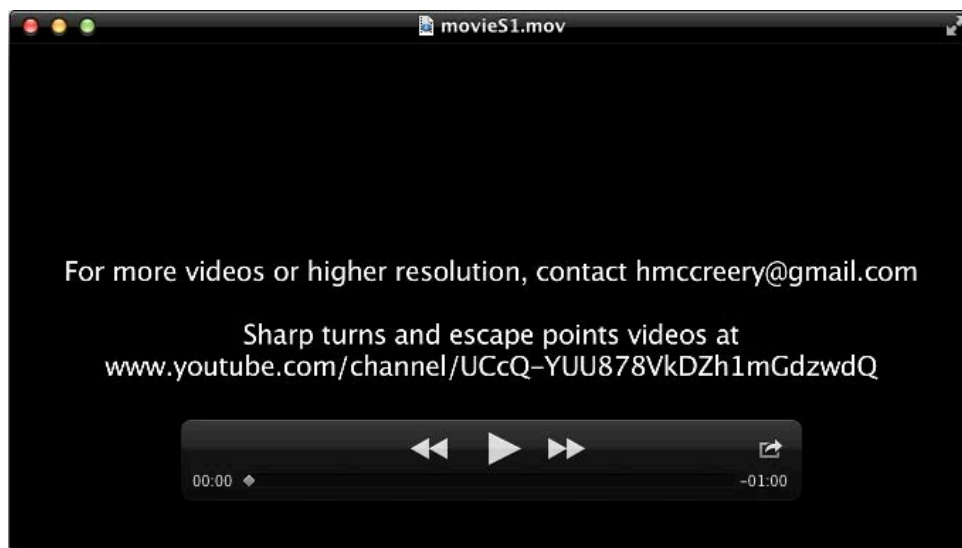
Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.143818.supplemental>

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Supplementary information



Movie S1: **Videos of trials for the examples shown in Fig. 2, panels A and C.** For higher resolution and additional videos, including an extended version of this video and videos of sharp turns and escape points, go to <https://youtu.be/vN4P8tq5DVw>, <https://youtu.be/-gz3tUbTpdU>, or <https://youtu.be/LcYkzdDh10Q>, respectively.

Table S1: Results of model selection for speeds.

Predictors	Δ AIC
Full model: Which.Obstacle + In.Obstacle? + Interaction + Random effect of trial nested within colony	16.4
Which.Obstacle + In.Obstacle? + Random effect of trial nested within colony	6.43
Which.Obstacle + Random effect of trial nested within colony	367
In.Obstacle? + Random effect of trial nested within colony	0
Random effect of trial nested within colony only	362

Table S2: Details of best-fit model for speeds. All coefficients are reported for square-root-transformed data.

		Value
Intercept		0.662
Random effects on intercept	Variance among colonies	0.018
	Variance within trials	0.011
Fixed effect	In.Obstacle?Yes (Coefficient acts on speeds while navigating obstacle)	-0.065

Table S3: Details of model results for Bayesian analysis of backward runs. Posterior means are shown and 95% credible intervals in parentheses.

	Wall	Cul-de-sac	Trap
β	0.0019 (-0.15 – 0.15)	0.14 (0.07 – 0.20)	-0.22 (-0.26 – -0.19)
α_i mean	-0.39 (-0.64 – -0.14)	-0.58 (-0.74 – -0.42)	-0.58 (-0.72 – -0.44)
α_i standard deviation	0.42 (0.25 – 0.65)	0.27 (0.16 – 0.44)	0.29 (0.20 – 0.42)
θ (scale parameter)	36 (28 – 44)	11 (9.7 – 12)	33 (31 – 36)

Supplementary information continues on the next page.

Supplementary figures

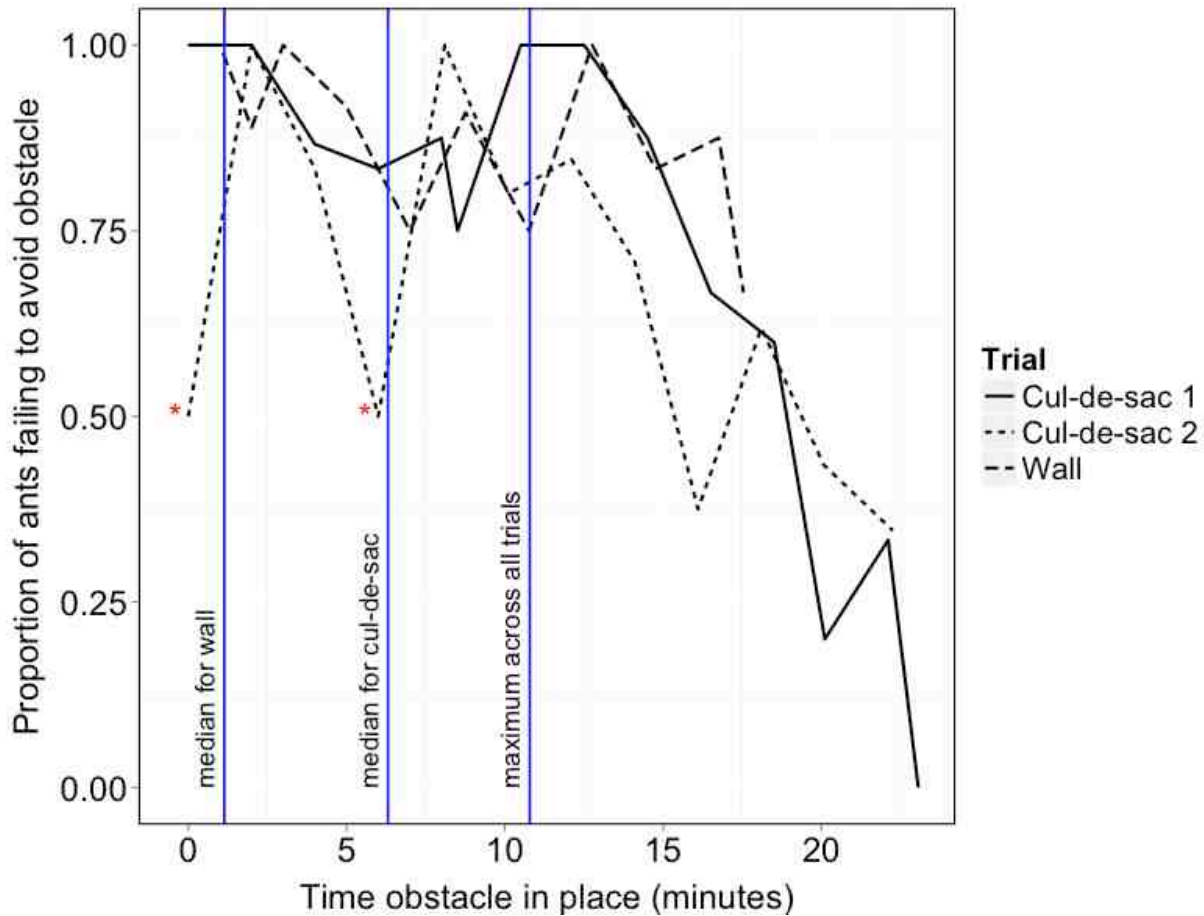


Fig. S1: **Response of individual ant paths to obstacles over time.** Obstacles were placed in the path of ants returning from sugar water baits. Shown here are the proportions of ants forced to navigate the obstacle because they failed to avoid it, measured in 10 second increments every two minutes. The “Cul-de-sac 2” trial had low traffic for the first several minutes; the two points marked with red asterisks each represent just 1 ant hitting the obstacle and 1 ant avoiding. The other data points in the Cul-de-sac 2 trial were based on an average of 15.7 ants per data point, while there were an average of 10.7 ants and 8.5 ants per data point, respectively, for the Wall trial and Cul-de-sac 1. Vertical lines show the median and maximum lengths of time obstacles were in place during trials for our main experiments. Our trials did not last long enough to be substantially affected by avoidance cues.



Fig. S2: Trajectories of groups of ants navigating the wall for all trials (n = 22). Warmer colors indicate earlier in time, cooler colors indicate later in the navigation process.



Fig. S3: Trajectories of groups of ants navigating the cul-de-sac for all trials (n = 19).
Warmer colors indicate earlier in time, cooler colors indicate later in the navigation process.



Fig. S4: **Trajectories of groups of ants navigating the trap for all trials (n = 20).** Warmer colors indicate earlier in time, cooler colors indicate later in the navigation process.

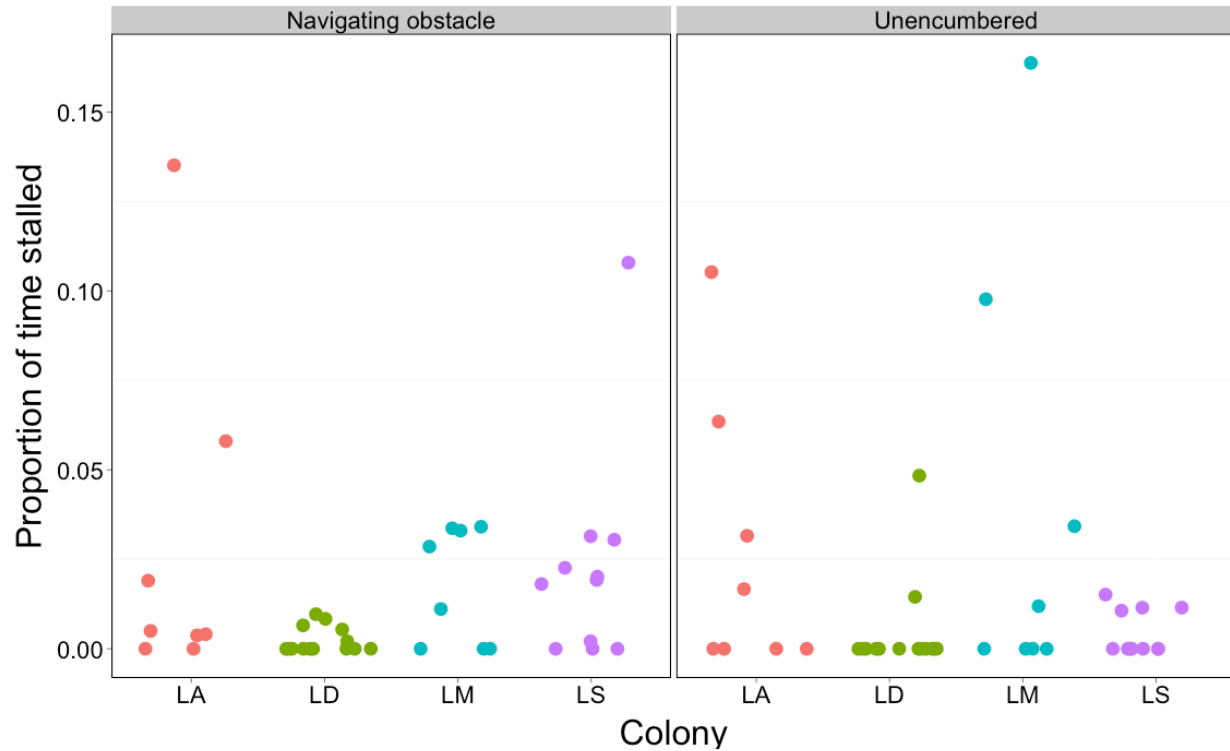


Fig. S5: **Proportions of time stalled in each trial while navigating the obstacle (left panel) and while unencumbered (right panel).** Groups spend approximately equal proportions of time stalled regardless of whether they are obstructed or not. Proportions of time stalled do not substantially differ among colonies. LA and LD are colonies at Arizona State University, LM and LS are colonies at Biosphere 2.

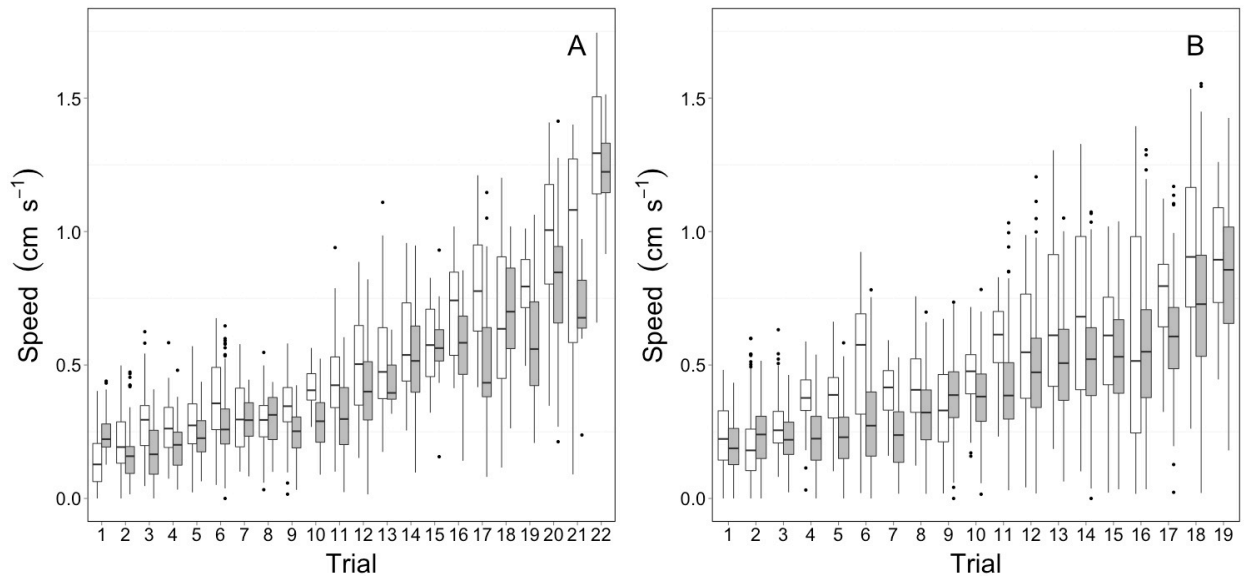


Fig. S6: Mean speeds for groups navigating an obstacle (gray boxes) and while unobstructed (open boxes) for each trial. A: trials with the wall; B: trials with the cul-de-sac. Boxes include 50% of the data (going from the 25th to 75th percentiles), and whiskers extend to the lowest and highest values that are within 150% of the interquartile range. Dots are points outside that range. The best general linear model of speeds, determined using AIC, included whether the group was obstructed ($\beta = -0.065$) and a random effect of trial nested within colony. While speeds were reduced during obstacle navigation, the reduction in speed was only 10% on average, and amounted to a small change compared with the variation in speeds across trials.

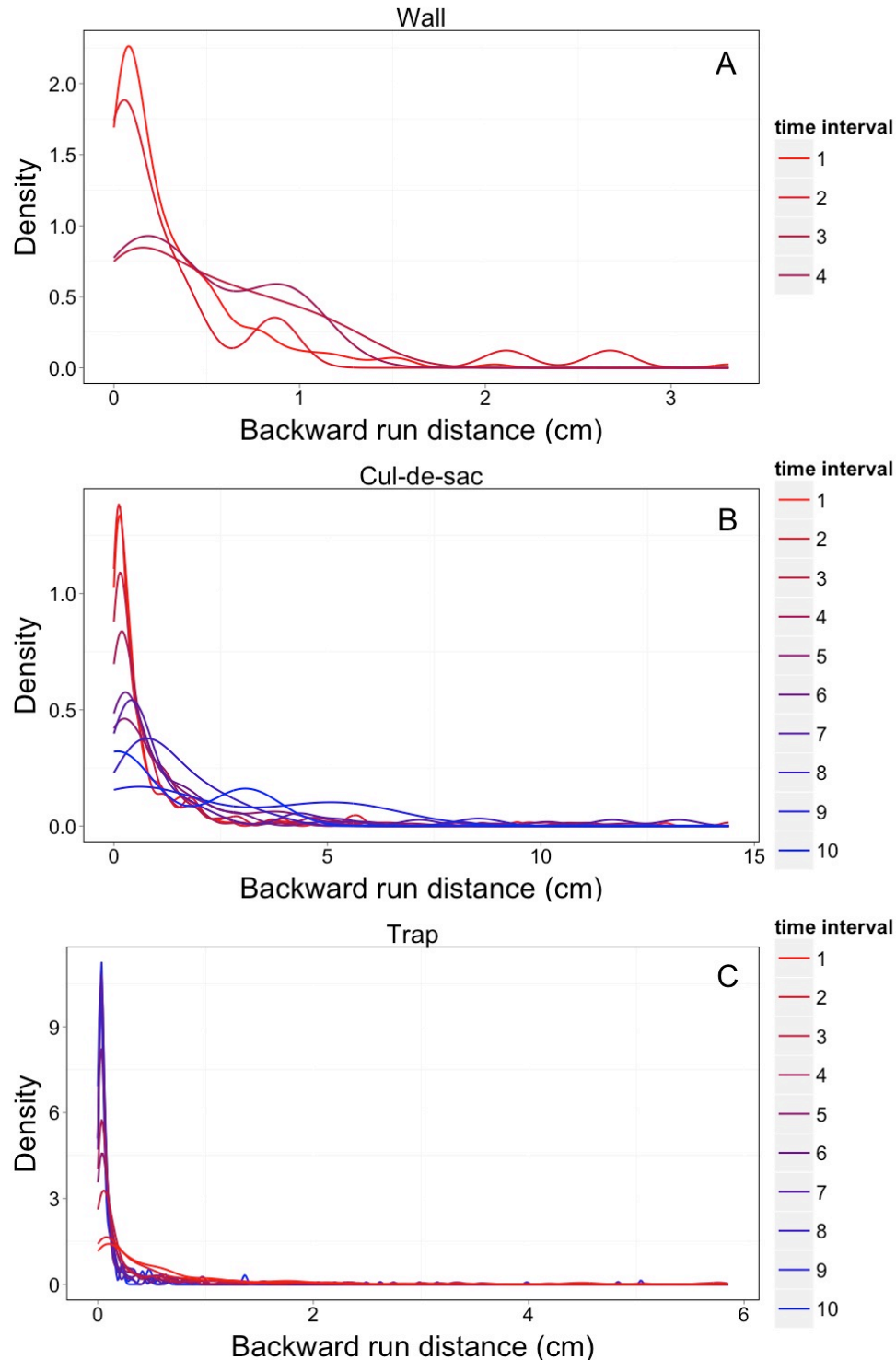


Fig. S7: Densities of backward run distances of groups navigating obstacles at different time intervals. A: the wall; B: the cul-de-sac; and C: the trap. Each time interval is 67 seconds long (one-tenth the total time across all trials). Warmer colors indicate earlier time intervals, and cooler colors are later time intervals. Modeled in a Bayesian framework as a gamma distribution

with a changing shape parameter, our estimate of the effect of time, β , in the cul-de-sac (B), is 0.13 (95% CI: 0.07 – 0.20). Thus, in the cul-de-sac, groups move further away from the nest the longer they have been navigating. We did not find strong evidence for this effect in the wall (A; $\beta = 0.0019$, 95% CI: -0.15 – 0.15), and found the opposite effect in the trap (C; $\beta = -0.22$, 95% CI: -0.26 – -0.19). The distribution of distances of backwards runs becomes more right-skewed over time in the cul-de-sac but not the other obstacles.

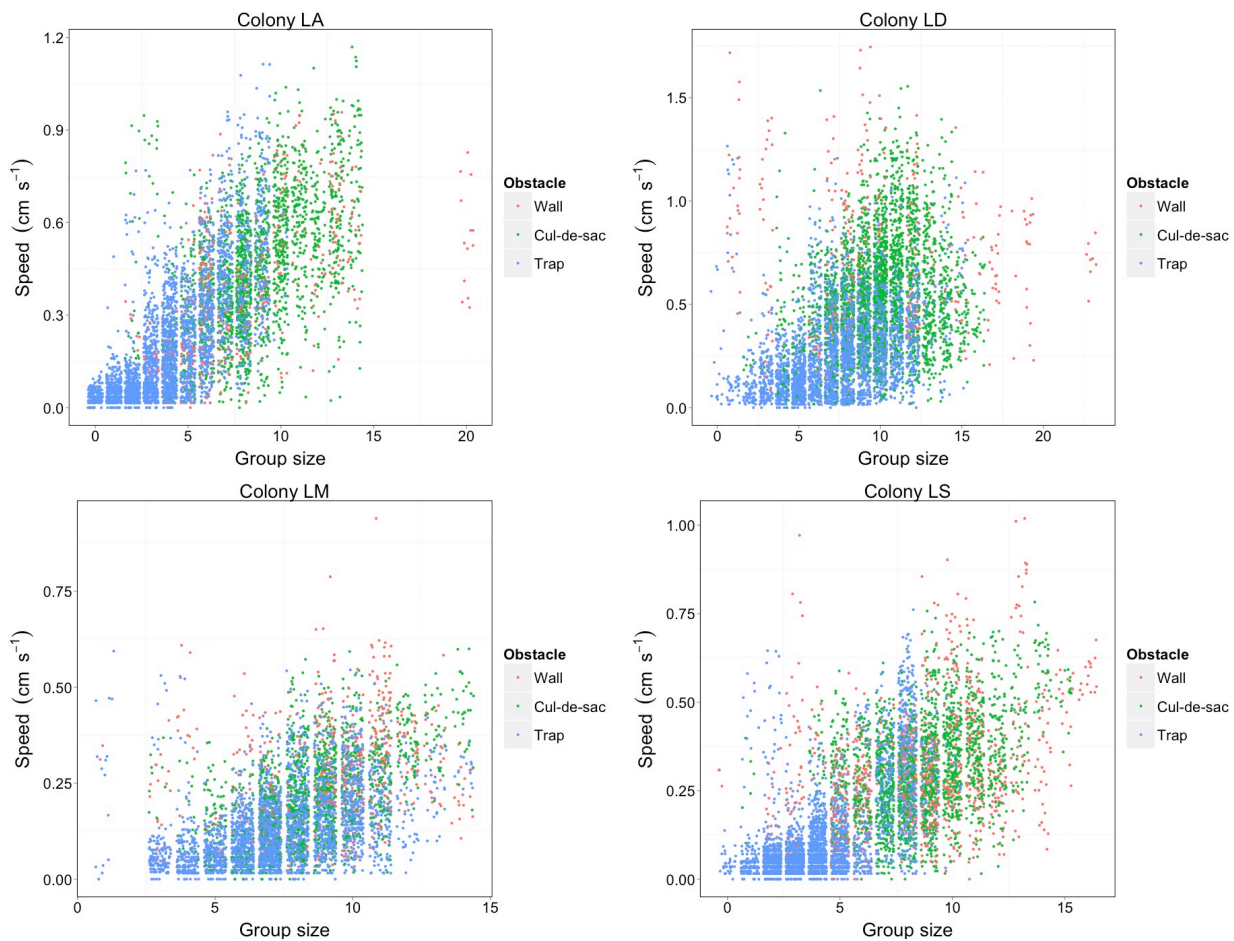


Fig. S8: **Speeds of groups at different group sizes.** Group sizes are jittered. Speed is positively correlated with group size, and this effect is consistent across colonies (Kendall's $\tau = 0.44$, $P < 0.0001$).

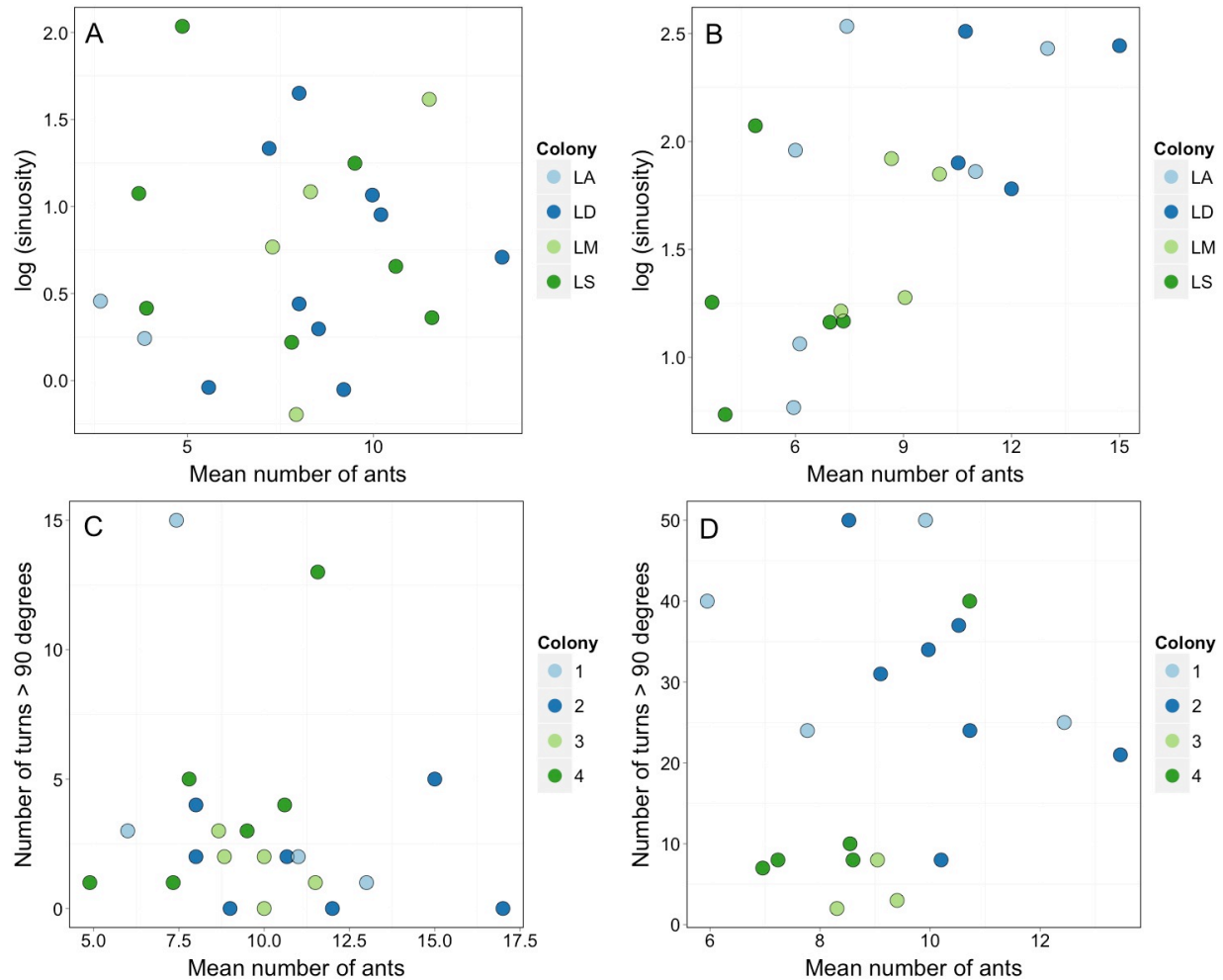


Fig. S9: Neither sinuosity nor number of direction changes are not correlated with the mean number of ants (group size). A and B: Sinuosity in the wall (Pearson's $r = -0.18$, $P = 0.43$) and cul-de-sac (Pearson's $r = 0.25$, $P = 0.30$), respectively. C and D: Number of direction changes in the wall (Kendall's $\tau = -0.19$, $P = 0.25$) and the cul-de-sac (Kendall's $\tau = 0.17$, $P = 0.36$), respectively. Blue dots are points for colonies at Arizona State University (light blue: colony LA; dark blue: colony LD) and green dots indicate colonies at Biosphere 2 (light green: colony LM; dark green: colony LS).

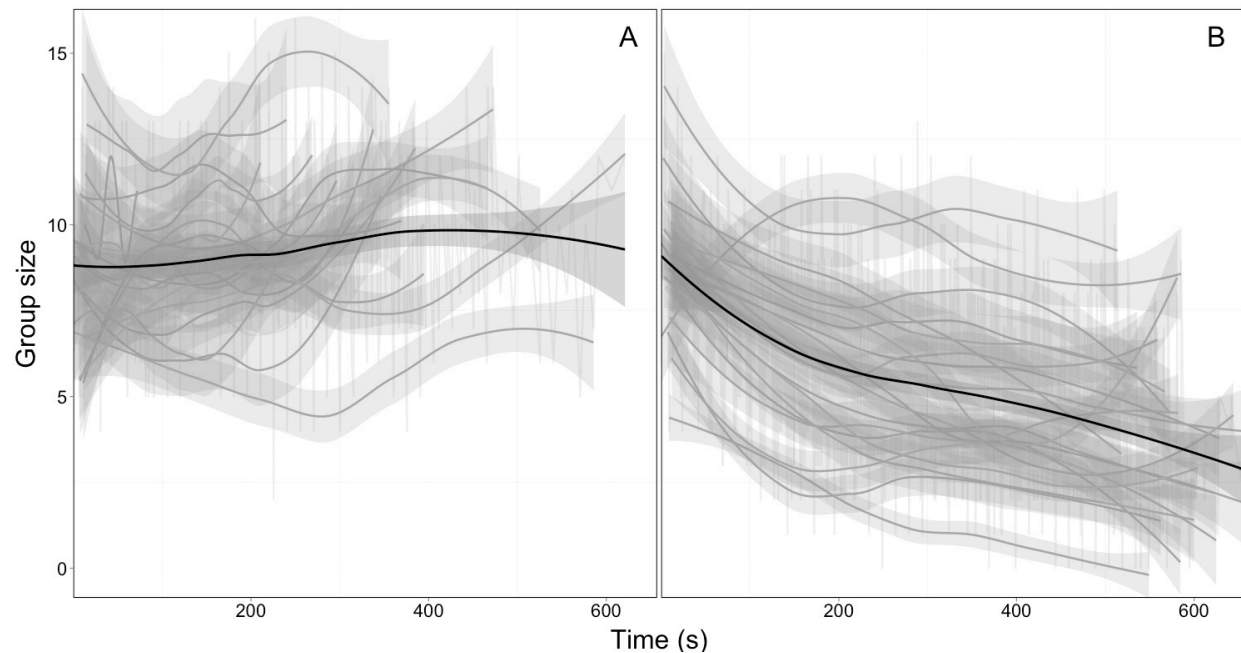


Fig. S10: **Group sizes over time of groups navigating the cul-de-sac (A) and in the trap (B).** Group size reduced in the trap dramatically, as individuals spent less time grasping the object. Groups in the cul-de-sac maintain relatively constant group sizes. Light grey, unsmoothed lines (background) show raw speed data. Grey, smooth lines show the smoothed speed for each trial and black lines show smoothed speed across trials, all computed with LOESS.

