

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/335076930>

Effects of load mass and size on cooperative transport in ants over multiple transport challenges

Article in *Journal of Experimental Biology* · August 2019

DOI: 10.1242/jeb.206821

CITATIONS

0

READS

92

4 authors, including:



Helen McCreery

Harvard University

22 PUBLICATIONS 90 CITATIONS

SEE PROFILE



Michael D Breed

University of Colorado Boulder

303 PUBLICATIONS 5,021 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Consensus or Deadlock? Consequences of Simple Behavioral Rules for Coordination in Group Decisions [View project](#)

RESEARCH ARTICLE

Effects of load mass and size on cooperative transport in ants over multiple transport challenges

Helen F. McCreery^{1,*}, Jenna Bilek², Radhika Nagpal^{1,3} and Michael D. Breed²

ABSTRACT

Some ant species cooperatively transport a wide range of extremely large, heavy food objects of various shapes and materials. While previous studies have examined how object mass and size affect the recruitment of additional workers, less is understood about how these attributes affect the rest of the transport process. Using artificial baits with independently varying mass and size, we reveal their effects on cooperative transport in *Paratrechina longicornis* across two transport challenges: movement initiation and obstacle navigation. As expected, object mass was tightly correlated with number of porters as workers adjust group size to the task. Mass affected performance similarly across the two challenges, with groups carrying heavy objects having lower performance. Yet, object size had differing effects depending on the challenge. While larger objects led to reduced performance during movement initiation – groups took longer to start moving these objects and had lower velocities – there was no evidence for this during obstacle navigation, and the opposite pattern was weakly supported. If a group struggles to start moving an object, it does not necessarily predict difficulty navigating around obstacles; groups should persist in trying to move ‘difficult’ objects, which may be easier to transport later in the process. Additionally, groups hitting obstacles were not substantially disrupted, and started moving again sooner than at the start, despite the nest direction being blocked. *Paratrechina longicornis* transport groups never failed, performing well at both challenges while carrying widely varying objects, and even transported a bait weighing 1900 times the mass of an individual.

KEY WORDS: Emergent behavior, Self-organization, Decentralized coordination, Collective behaviour, Formicidae

INTRODUCTION

Social collectives are remarkably successful, with ants being among the most cooperative and most dominant animal groups (Hölldobler and Wilson, 1990). Cooperative transport – working together to move large food or other objects – is a key element leading to the ecological success of some ants, as it increases the range of food resources that groups can exploit (Czaczkes and Ratnieks, 2013; Feinerman et al., 2018; McCreery and Breed, 2014; Wojtusiak et al., 1995). *Paratrechina longicornis* is among the most widely dispersed species (Wetterer, 2008; Wetterer et al., 1999) and is

also particularly adept at transporting foods cooperatively (Czaczkes and Ratnieks, 2013; Feinerman et al., 2018; Fonio et al., 2016; Gelblum et al., 2015), which may partially account for the success of this species in diverse ecosystems.

To perform cooperative transport, groups must contend with multiple challenges which may require different collective behaviours. After assembling at a food item, a group must make a collective decision about travel direction and overcome friction to initiate movement of the object. Once moving, they must maintain directional consensus while navigating to their nest. Homeward navigation is affected by the complexity of the environment, which includes obstacles that block the group’s path. These two challenges (initiating movement and navigating around obstacles) translate, though imperfectly, to the ‘organization’ and ‘transport’ phases of cooperative transport as outlined in McCreery and Breed (2014). Here, we refer to these cooperative transport phases as movement initiation and obstacle navigation, respectively. The nature and difficulty of these phases depend on the item being transported. How do object properties, such as size and mass, affect group performance by *P. longicornis* in the different challenges of the transport process?

We have only a limited understanding of how transport mechanisms and behaviours interact with different cooperative transport phases. Previous mechanistic studies have looked primarily at a particular phase; for example, at the recruitment phase (Czaczkes and Ratnieks, 2012; Daly-Schweitzer et al., 2007; Robson and Traniello, 1998), or at how groups actively move toward the nest (Buffin and Pratt, 2016; Fonio et al., 2016; Gelblum et al., 2015; McCreery et al., 2016b). Even for behaviours within a particular phase, our understanding of how object properties affect performance is relatively poor. Several studies have observed the masses of natural objects typically carried by groups (Franks, 1986; Franks et al., 1999, 2001; Moffett, 1988; Traniello and Beshers, 1991) and/or provided bait objects of multiple sizes (Moffett, 1988; Robson and Traniello, 1998; Traniello and Beshers, 1991). From these studies, we have learned about how object size overall affects or is correlated with group composition or delivery rate, for example, but these studies did not isolate the effect of mass from other attributes, like size. Army ants are among the species for which we understand the most about how object mass affects transport dynamics (Franks, 1986; Franks et al., 1999, 2001), yet the cooperative transport of army ants differs substantially from cooperative transport in most ants, as they use ‘forward-facing’ rather than ‘encircling’ transport (Czaczkes and Ratnieks, 2013). A number of more recent experiments have provided detailed, mechanistic analyses of cooperative transport dynamics, in species with encircling transport, but have typically tried to remove the potential influence of object properties by providing groups with essentially uniform baits (Berman et al., 2011; Buffin and Pratt, 2016; Czaczkes et al., 2011; Fonio et al., 2016; Kumar et al., 2013; McCreery et al., 2016b; Robson and Traniello, 2002). We still lack a clear understanding of how object properties

¹School of Engineering and Applied Sciences, Harvard University, Cambridge, MA 02138, USA. ²Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA. ³Wyss Institute, Harvard University, Boston, MA 02115, USA.

*Author for correspondence (hmccreery@seas.harvard.edu)

 H.F.M., 0000-0003-3811-7960; M.D.B., 0000-0002-4039-8354

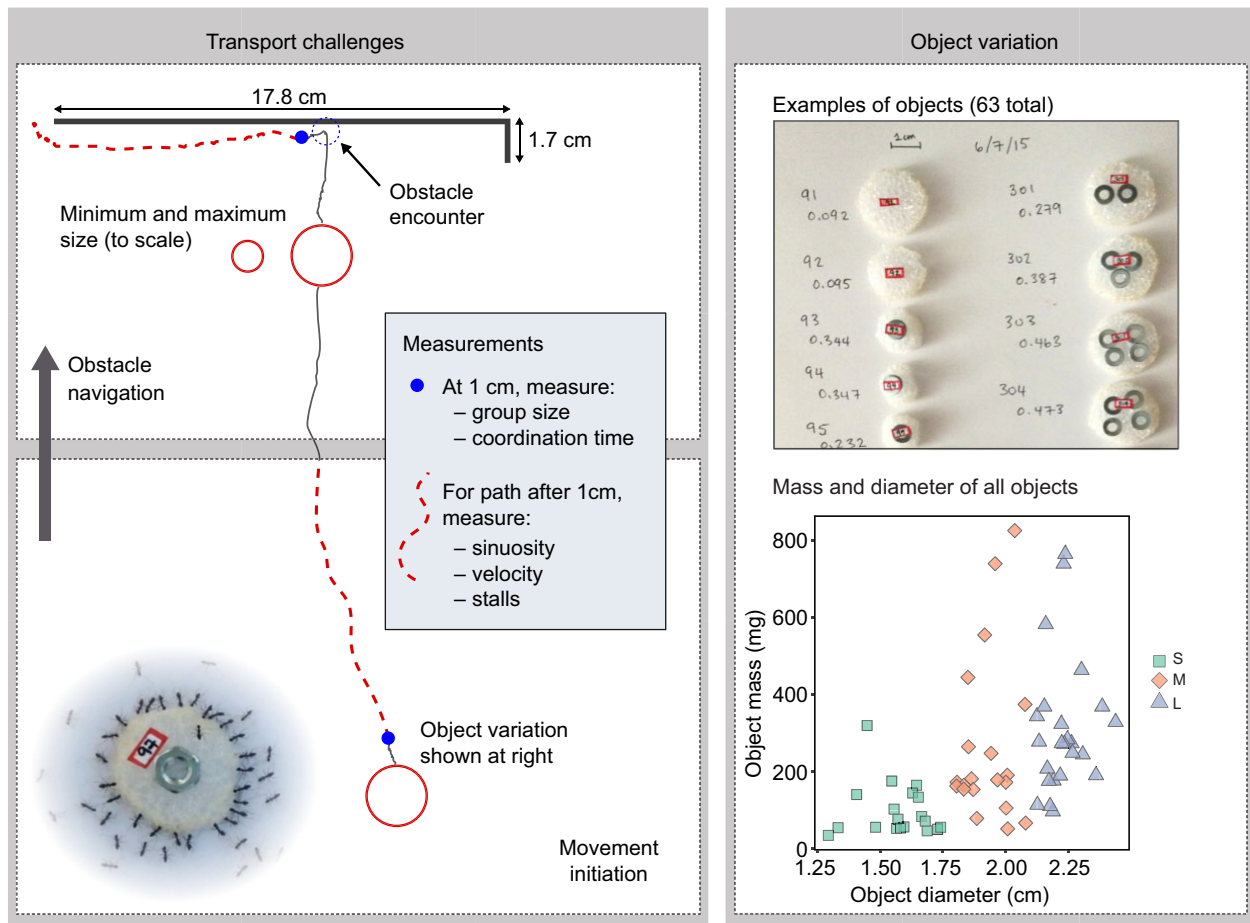


Fig. 1. Conceptual diagram for experiments. Experimental process and measurements are shown on the left; variation in objects is shown on the right.

independently affect cooperative transport across the differing challenges that it entails.

We systematically varied object mass and size and explored the consequences of this variation in two phases of cooperative transport: movement initiation and obstacle navigation. We provided colonies with bait objects varying over a large range in mass and size (Fig. 1) with the goal of discovering how these variables affect group size. We collected multiple measures of transport performance: coordination time (time to move), sinuosity

(or path tortuosity), velocity and proportion of time stalled. We examined these variables during two important challenges within each transport event, movement initiation and navigation around an obstacle (Fig. 1). Our hypotheses about the effects of object variation on transport are summarized in Table 1. We expected relationships between object properties and transport performance to be similar at movement initiation and during obstacle navigation. We also predicted that performance measures overall would be lower during obstacle navigation as a result of the navigational

Table 1. Hypothesis table, including predicted transport performance and rationale, for effects of object variation (mass and size) on group size and performance

| Metric | Object mass | Object size |
|-----------------------------|---|--|
| Group size | Positive effect. Heavier objects should require larger groups to move them. | Positive effect. Larger objects can fit more ants around them and may require more ants as a result of object stability. |
| Coordination time | Positive effect. If each ant must carry a heavier load, it may take longer for groups to align forces and coordinate. | Positive or negative effect. Stability issues or larger groups may slow down coordination. Alternatively, large groups may coordinate faster (McCreery et al., 2016a). |
| Sinuosity (path tortuosity) | Positive effect (higher mass decreases performance). Groups carrying heavier loads may stop and start, leading to direction changes. | Positive or negative effect. Stability issues or larger groups may require more stops and starts, increasing sinuosity. Alternatively, larger groups may have improved coordination (see above). |
| Velocity | Negative effect. Groups with heavier loads should move slower. If these groups have higher sinuosity, this will also decrease velocity for the trial. | Positive or negative effect. Stability issues may slow groups down. Larger groups may move faster or slower, depending on how group size affects coordination (see above). |
| Proportion of time stalled | Positive effect (higher mass lowers performance). Groups carrying heavier loads may stop and start. | Positive or negative effect. Stability issues or larger groups may require more stops and starts. Larger objects may also enable improved coordination (see above). |

challenge. Our results shed light on the mechanisms allowing *P. longicornis* collectives to succeed so convincingly at this task across a wide variety of objects.

MATERIALS AND METHODS

Experiments

We provided *P. longicornis* (Latreille 1802) colonies with baits, described below, that differed only in size and mass, with a large range in mass among baits of a given size. For each trial, we recorded groups as they began transport; after transport was established, we blocked each group with an obstacle and recorded navigation attempts. All experiments were conducted in the field, at locations adjacent to six different *P. longicornis* colonies at the Arizona State University campus in Tempe, AZ, USA.

We set up trials on smooth, flat surfaces (such as concrete) near a single nest entrance, so that all recruits had the same goal. We taped white paper to the ground, replacing it between each trial, to remove possible effects of pheromones on subsequent trials. We placed a large cricket (killed by freezing) on the paper to elicit a strong recruitment response. The distance to the nest was not standardized, and we waited to begin each trial until a group was successfully moving this cricket, to ensure that there were sufficient workers in close proximity to the bait. This allowed us to disentangle coordination time from recruitment time, and also reduced the effects of the number of available porters. When the cricket was being moved successfully, we replaced it with one of the experimental baits. While this replacement disturbed the ants, the disturbance lasted only seconds, as porters readily grasped the newly placed bait object. After the group left the video frame, we blocked their path with an obstacle and used a separate video-recording system to record obstacle navigation. Baits were not re-used between trials. We recorded all trials using an Apple iPod touch. Example trials are shown in Movie 1.

Baits

Baits were disks, constructed from rigid craft foam. To make baits attractive, we applied a uniform volume of tuna-permeated oil – from tuna packed in olive oil – to the circumference of each bait. Tuna is a commonly used ant bait that elicits group transport behaviour in *P. longicornis* (McCreery et al., 2016b). Baits were allowed to dry before use, with oil absorbing into the object, and always elicited vigorous transport attempts from *P. longicornis* workers. Bait diameter ranged from 1.29 to 2.44 cm, and mass ranged from 34 to 825 mg (Fig. 1). We altered the mass of baits by gluing one or more objects on top of the disks, such as plastic beads and small metal washers and nuts. Summary statistics for the baits, categorized into three size classes, are given in Table 2. While we were not able to make the largest disks as light as the lightest small disks, nor the smallest disks as heavy as the heaviest large disks, there was a large range in mass within each size class, as shown in Fig. 1 (bottom right). Example baits are also shown in Fig. 1 (top right).

Obstacle

We used the same obstacle for all trials (Fig. 1): a 17.8 cm wall with a 90 deg corner on one side. Despite this asymmetry, groups chose

each direction with approximately equal probability, both in their initial choice of travel direction (48% toward angled side and 52% toward straight side) and in the side they finally moved around the obstacle (44% angled side and 56% straight side). The bottom of the obstacle was coated with Insect-a-Slip (Fluon, BioQuip, Gardena, CA, USA) to prevent groups from climbing over it. We waited to place the obstacle until the group was within 5 cm, blocking the group with the obstacle such that it was perpendicular to the direction of travel, making their preferred direction unavailable.

Data extraction

All data and code are publicly available on figshare (McCreery et al., 2019). We extracted several kinds of data from the videos by manually recording the location and orientation of the bait every second using Matlab. We used these trajectories to measure coordination time, velocity, sinuosity and the proportion of time the group stalled. We defined coordination time as the time it took the group to move the bait 1 cm, either after the bait was put down or, during obstacle navigation, after the group hit the obstacle. Thus, coordination time does not include recruitment time. At 1 cm, all groups were successfully moving smoothly, whereas distances of the order of 1 mm were sometimes reached haltingly. We also measured sinuosity, which is the total path length divided by the displacement. Paths with lower sinuosity indicate more coordinated groups. For each recording, we measured velocity as the displacement of the group over the whole recording (rather than path length) divided by the time elapsed since the group had moved 1 cm. Thus, coordination time is not included in the velocity measurement. We chose this velocity measure, rather than using a mean instantaneous speed, because it provides more direct information about how quickly groups can reach their nest. As we calculated velocity using displacement, which is similar across recordings of obstacle navigation (approximately half the obstacle width), this metric is also roughly proportional to obstacle navigation time, which we did not separately analyse. Finally, we examined the proportion of time the group was stalled, again recording from the time the group had moved 1 cm. We defined a stall as a time during which the group's instantaneous speed was below 0.012 cm s^{-1} , which we chose because actively moving groups did not move that slowly, but it was high enough that pixel-sized trajectory errors did not result in categorizing stalls as movement. In two trials, the group interacted with part of the camera support during the movement initiation phase. We excluded the sinuosity measurements for these trials. We also excluded the sinuosity measurement for one trial in which the group left and re-entered the frame.

In addition to these metrics, we measured the group size when successful movement began. To find this, we counted the number of ants attached to the bait when the group had just moved 1 cm, either at the beginning of movement or after hitting the obstacle. We explored whether object mass and size affect group size, and we examined the effects of size and mass per ant on other performance measures (we did not separately examine the effects of group size and mass on performance because of a strong correlation between these variables).

Statistical analyses

All analyses were performed in R version 3.4.1 (<http://www.R-project.org/>), using tidyverse (<https://CRAN.R-project.org/package=tidyverse>) and nlme (<https://CRAN.R-project.org/package=nlme>) packages. For each response variable, we conducted three statistical analyses: evaluating the effects of object properties during movement

Table 2. Summary statistics for baits in each size class

| Size class | Sample size | Mean±s.e.m. diameter (cm) | Mean±s.e.m. mass (mg) |
|------------|-------------|---------------------------|-----------------------|
| Small | 19 | 1.57±0.029 | 98±16 |
| Medium | 20 | 1.93±0.020 | 264±48 |
| Large | 24 | 2.23±0.017 | 308±36 |

initiation, evaluating the effects of object properties during obstacle navigation, and comparing the response variable across these two phases. Our overall approach was to use likelihood (corrected Akaike information criterion, AICc) to determine which predictors are most important. If a single statistical model clearly outperformed other candidate models, we based inference on this model alone. If multiple candidate models performed similarly, we used Akaike weights to infer which predictors are important, as discussed in more detail below.

When analysing the effects of object properties during initiation and obstacle navigation, we used linear mixed-effects models on log-transformed response variables to identify important predictors. Log transformation of response variables was sufficient to meet assumptions of normality. Each full model incorporated two possible predictors (object size and either object mass or mass per ant) and their interaction, and we used AICc to select the most likely among possible models. We excluded models with only interaction terms without the main effects but included null models with no predictors. In all candidate models, colony was included as a random effect acting on the intercept. For each response variable, we based inference solely on the best model if only one candidate model had $\Delta\text{AICc} < 2$. If the null model had $\Delta\text{AICc} < 2$, we inferred that neither predictor was important. For some analyses we had substantial model uncertainty, as there were multiple models with $\Delta\text{AICc} < 2$, excluding the null. In these cases, we considered all such models, using Akaike model weights and predictor weights (calculated with the full complement of models) to infer the predictors most likely to be important. This approach is appropriate when there is model uncertainty, as in such cases it is misleading to draw inference from any single model (Lukacs et al., 2010; Symonds and Moussalli, 2011). For all analyses, we evaluated the appropriateness and fit of all models with $\Delta\text{AICc} < 2$ using diagnostic plots of predictors and residuals. Because of a strong correlation between mass and group size (see Results), we did not include both of these predictors in models of performance measures. Instead, we combined these variables into a single predictor, mass per ant. Object size was treated as a continuous variable for all analyses (measured as disk diameter), but for clarity, in some figures we categorized sizes into small, medium and large.

To directly compare responses during movement initiation and obstacle navigation, we again used linear mixed-effects models. We included challenge type, or phase, as a possible predictor (start or

obstacle), and had random effects of trial nested within colony, acting on the intercept. We used AICc to compare the model including 'phase' with a null model, and we evaluated final models using diagnostic plots of predictors and residuals.

RESULTS

Group size

Object mass and size are positive predictors of porter group size, with mass having a larger effect (Fig. 2). This was true both for movement initiation and for obstacle navigation, with similar predictor coefficients; in each case, the model including mass and size was the only model with ΔAICc less than 2 (Table 3; Fig. S1 and Tables S1, S2 and S3). As discussed above, because of the strong correlation between mass and group size, we did not include these predictors separately in other models, instead including 'mass per ant'. Group size increased slightly from movement initiation to obstacle navigation and the null model, excluding transport phase, performed poorly ($\Delta\text{AICc}=26$; Table S1). The mean (\pm s.e.m.) group size was 12.5 ± 0.92 at the beginning of movement and 15.3 ± 0.83 during obstacle navigation (Fig. 2C).

Coordination time

At movement initiation, groups carrying objects with higher mass per ant and groups carrying larger objects each took longer to begin moving (Fig. 3A,B, Table 3). Only the model including positive effects of mass per ant and object size, with no interaction, had $\Delta\text{AICc} < 2$. Mass per ant affected coordination time more strongly ($\beta=62.1$ compared with $\beta=1.6$ for object diameter), yet models excluding the size effect performed poorly.

For obstacle navigation, there were three models with $\Delta\text{AICc} < 2$: the full model, the model including only mass per ant, and the model including mass per ant and size. Because of this model uncertainty, we used Akaike weights to base our inference on all three models, and we do not report a single effect size for a given predictor. Coefficients for each model with $\Delta\text{AICc} < 2$ are included in Table 3. Mass per ant had a combined Akaike weight of 1.00 (Table S2), interpretable as an approximately 100% chance that mass per ant is a component of the best model, and this effect was always positive. Thus, consistent with the results for the start of movement, groups that encounter higher mass per ant take longer to begin moving after hitting an obstacle (Fig. 3C).

Object size was less important, with an Akaike weight of 0.63 (63% chance) and this effect was always negative, while the

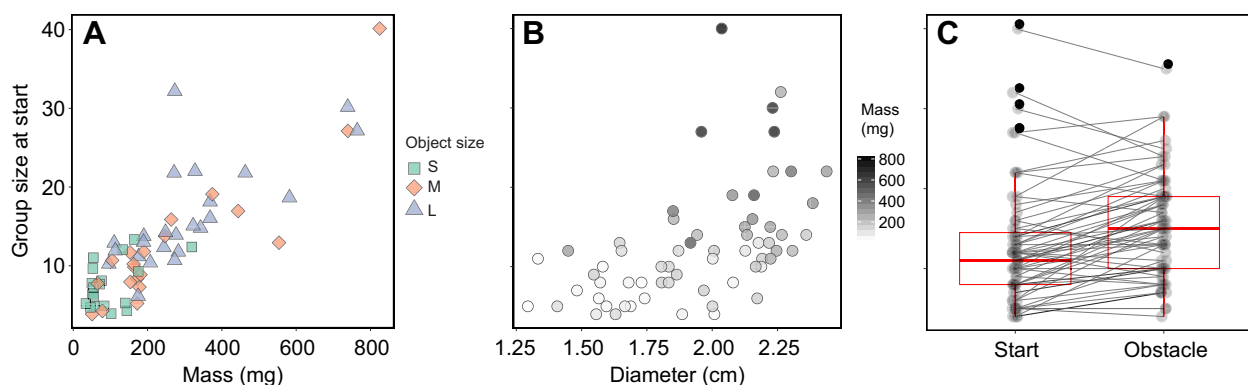


Fig. 2. Effect of object mass and diameter on size of cooperative transport groups. Group size was measured at the point the groups had moved 1 cm during the initiation of movement ($N=63$). (A) Effect of object mass on group size ($\beta=1.84$) for objects of different size. (B) Effect of object diameter on group size ($\beta=0.60$) for objects of different mass. (C) Group size comparison at the start and during obstacle navigation. Lines connect start and obstacle measures for the same trial. Model details are included in Table 3 and Tables S1, S2 and S3.

Table 3. Summary of statistical results evaluating the effects of object properties, including all models with $\Delta AICc < 2$

| Predictors | Coefficients | | | $\Delta AICc$ |
|---|--------------|-------|-------------|---------------|
| | Mass or MPA | Size | Interaction | |
| Group size: movement initiation | | | | |
| Mass+size | 1.84 | 0.60 | | 0 |
| Group size: obstacle navigation | | | | |
| Mass+size | 1.25 | 0.63 | | 0 |
| Coordination time: movement initiation | | | | |
| MPA+size | 62.1 | 1.61 | | 0 |
| Coordination time: obstacle navigation | | | | |
| MPA+size+MPA:size | 78.8 | -0.24 | -43.3 | 0 |
| MPA | 80.3 | | | 0.174 |
| MPA+size | 82.4 | -0.24 | | 1.12 |
| Sinuosity: movement initiation | | | | |
| MPA | 8.49 | | | 0 |
| MPA+size | 7.81 | 0.12 | | 0.949 |
| Sinuosity: obstacle navigation | | | | |
| Size | -0.39 | | | 0 |
| Null* | | | | 0.636 |
| MPA+size | 7.24 | -0.43 | | 1.63 |
| Velocity: movement initiation | | | | |
| MPA+size | -62.2 | -0.45 | | 0 |
| MPA | -65.6 | | | 1.65 |
| Velocity: obstacle navigation | | | | |
| MPA | -48.1 | | | 0 |
| MPA+size | -49.9 | 0.23 | | 1.97 |

MPA, mass per ant. Complete statistical results for all models, including random effects estimates, model Akaike weights and weights for each predictor, are given in Tables S1, S2 and S3.

*Null model included in the set of models with $\Delta AICc < 2$; we infer that none of the possible predictors affect the response variable.

interaction had an Akaike weight of 0.40, also with a negative coefficient. Contrary to the pattern we found for movement initiation, for a given mass per ant, groups carrying larger objects seem to take less time to begin moving around an obstacle (Fig. 3D). This is hard to detect visually because of the multidimensionality of the experiment and the difficulty of visually observing patterns in data with mixed effects. Nevertheless, the statistical presence of this

effect is evident from the negative effect of object size on coordination time, and also from the negative interaction in the full model, indicating that the positive effect of mass per ant is lessened for larger objects. While there was a model with $\Delta AICc < 2$ that lacked an effect of size, we infer from the results of all the models that our data best support a positive effect of mass per ant and a weaker, negative effect of object size during obstacle

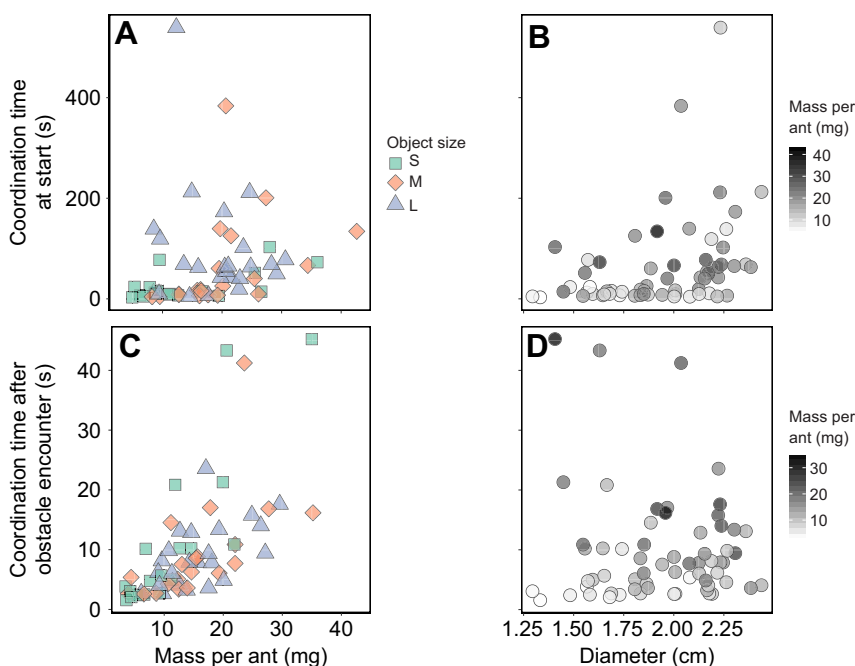


Fig. 3. Effects of object properties on coordination time (time to move 1 cm) during cooperative transport. (A,B) Effect of object mass per ant (A) and object diameter (B) during movement initiation ($N=63$, mass per ant $\beta=62.1$, diameter $\beta=1.6$). (C,D) Effect of object mass per ant (C) and object diameter (D) after hitting an obstacle ($N=63$, multiple high-performing models, results included in Table 3).

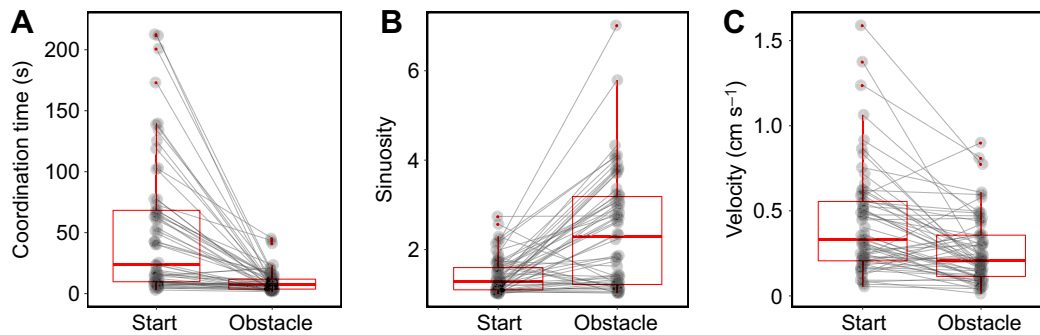


Fig. 4. Comparison of results during movement initiation and obstacle navigation. Lines connect start and obstacle measures for the same trial. (A) Coordination time ($N=63$ for each phase). For clarity, two trials with 'start' coordination data outside the y -axis range were excluded. These trials had coordination times of 539 and 387 s at the start, and 8 and 41 s, respectively, during obstacle navigation. (B) Sinuosity ($N=61$). (C) Velocity ($N=63$).

navigation. We infer that groups carrying larger objects take longer than groups carrying small objects to begin moving at the start but take less time to begin moving after hitting an obstacle.

Coordination time was also substantially lower during obstacle navigation than during movement initiation (ΔAICc for the null model excluding phase=56; Table S1). This difference cannot be attributed to the disturbance at the start caused by replacing the recruitment cricket with a bait, as the porters were only disturbed for a few seconds, while the difference was of the order of minutes. The mean (\pm s.e.m.) coordination time was 64 ± 11.6 s at the beginning of movement and only 9.7 ± 1.16 s during obstacle navigation (Fig. 4A).

Sinuosity

There were two models for sinuosity during movement initiation with $\Delta\text{AICc}<2$: the model including mass per ant and the model including mass per ant and object size (Table 3). These models had a combined Akaike weight of only 75%, and even the null model had a weight of 8% (Table S1). The Akaike weight for mass per ant was 0.83 and that for object size was 0.46, and both of these effects were positive where present (Fig. S1A,B). During obstacle navigation, neither mass per ant nor object size affected sinuosity, as the null model performed well, with $\Delta\text{AICc}=0.64$ (Fig. S1C,D). Sinuosity was substantially higher (paths less straight) during obstacle navigation than during movement initiation (ΔAICc for the null model=30; Table S1). The mean (\pm s.e.m.) sinuosity at the beginning of movement was 1.42 ± 0.052 and during obstacle navigation it was 2.39 ± 0.16 (Fig. 4B).

Velocity

Velocity was measured as the displacement of the object during the whole trial, divided by the time elapsed since the group moved 1 cm. For movement initiation, two models had $\Delta\text{AICc}<2$: the model including mass per ant and size, and the model including only mass per ant. Mass per ant had a combined Akaike weight of 1.00, and this effect was always negative; groups carrying heavier loads (per porter) moved more slowly (Fig. 5A). The Akaike weight for object size was 0.75, and this effect was also negative, indicating that larger objects are most likely carried more slowly right after movement initiation (Fig. 5B).

For obstacle navigation, models with the same two sets of predictors had $\Delta\text{AICc}<2$, but the effects were different. Mass per ant had an Akaike weight of 0.997, and this effect was negative, consistent with the results for the start of movement (Fig. S2A). Object size had an Akaike weight of 0.397, but this effect was positive, indicating that larger objects may be carried faster than smaller objects during obstacle navigation (Fig. S2B). While we cannot state this with high confidence, our results clearly do not support the negative effect we found at movement initiation. To explore this further, we visually examined grip space per mass, a measure of object density, calculated as the circumference of each object divided by its mass (see Fig. 5C). Small, heavy objects appear on the left side of this axis, while large, light objects are on the right. As heavy objects are likely to be carried by large groups, these groups will have more grip space carrying large objects than small objects, which may be reflected in higher velocities (Fig. 5C).

Finally, we found lower velocities during obstacle navigation than during movement initiation (ΔAICc for the null model=24;

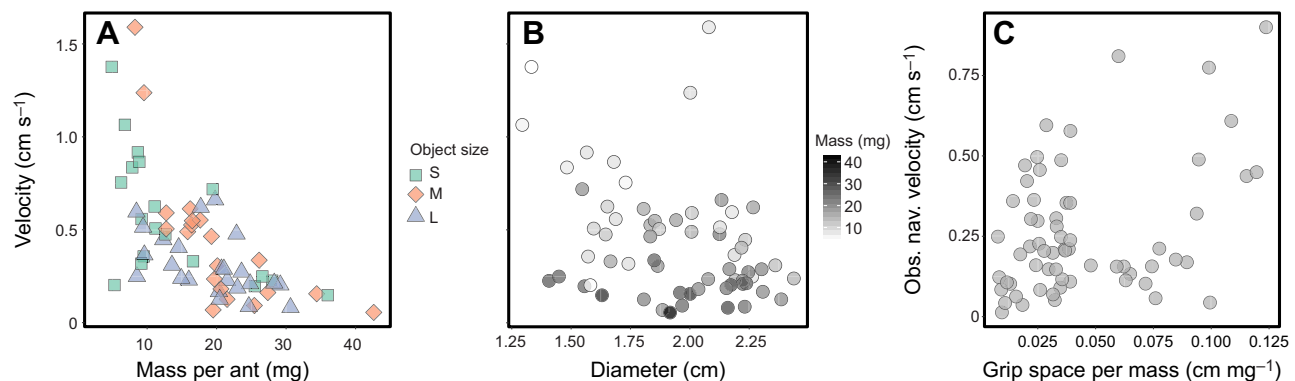


Fig. 5. Effects of object properties on velocity. (A,B) Effect of mass per ant (A) and object diameter (B) on movement initiation. (C) Obstacle navigation velocity versus grip space (object circumference) per mass ($N=63$).

Table S1). The mean (\pm s.e.m.) velocity at the beginning of movement was 0.43 ± 0.040 cm s⁻¹ and during obstacle navigation it was 0.26 ± 0.025 cm s⁻¹ (Fig. 4C).

Stalls

Groups rarely stalled; the mean (\pm s.e.m.) proportion of time stalled was $0.41\pm 0.20\%$ at the start and $1.1\pm 0.46\%$ during obstacle navigation (Fig. S3). We did not have enough trials with stalls to evaluate the effects of object properties on stalls or compare stalls across phases, whether using our initial thresholds or using more inclusive thresholds for counting a stall. *Paratrechina longicornis* groups rarely stall, even while carrying heavy loads and while navigating around obstacles.

DISCUSSION

Object properties affected transport performance in important ways in *P. longicornis*, and these effects depended on the performance measure and the transport phase: movement initiation or obstacle navigation. Our results show, unsurprisingly, that groups carrying objects with higher per capita mass had lower performance across both phases. Yet, the effects of object size varied; porter groups carrying larger objects had reduced performance during movement initiation but seemed to have higher performance for some measures during obstacle navigation. Previous research has not isolated object properties to carefully examine how they impact group behaviour. *Paratrechina longicornis* is highly invasive and colonies thrive in diverse environments; this success must be partially attributable to the fact that cooperative transport allows the ants to access a wide range of food resources. Our results help us to understand how these groups succeed at different transport challenges while carrying objects of varying mass and size.

Group size

Paratrechina longicornis collectives successfully transported every object we gave them, including a bait weighing 825 mg, which is over 1900 times the mean worker mass of 0.43 mg (McCreery, 2017). In part, groups succeeded by effectively matching group size to the object being carried. Unsurprisingly, heavier objects are carried by more porters. When groups began moving, their group size strongly reflected object mass (Fig. 2A), and variation in mass per ant was much smaller than variation in mass. These groups seem to move only after reaching a mass per ant below some threshold.

Group size is also constrained by object size, and indeed, we found that large objects were carried by larger groups than small objects, even for a given mass. One possible explanation for this relates to object stability. These groups lift objects they carry (Feinerman et al., 2018), and it is harder to lift larger objects from one side. Larger objects may require a more even distribution of workers around the object, which is more easily achieved with larger groups. Alternatively, this effect may simply be due to that fact that more porters can easily fit around larger objects; perhaps movement sometimes begins with larger groups than necessary. This mechanism could be directly tested in the future by controlling the distribution of ants around objects; for example, by using objects that can only be gripped on one side.

The effects of mass and size were similar during obstacle navigation, and group size slightly increased from movement initiation to navigation. Our results for group size qualitatively agree with results from observations of natural objects in other species, which found that larger and more massive objects are carried by more and/or more massive porters in *Eciton burchellii* and *Dorylus wilverthi* engaged in forward-facing cooperative transport (Franks,

1986; Franks et al., 1999), as well as *Pheidologeton diversus* engaged in encircling cooperative transport (Moffett, 1988). We add that for *P. longicornis*, this effect is attributable mostly to the mass of the objects, but that object size also independently affects group size. Fig. 2A is reproduced on a log scale as Fig. S4 to facilitate comparison with Franks (1986) and Franks et al. (1999). We excluded recruitment effects from our study to isolate the organization process, yet our results also still fit with previous research that looked explicitly at the recruitment phase, demonstrating in several species that more ants are recruited to bigger objects (Cerdá et al., 2009; Cogni and Oliveira, 2004; Daly-Schveitzer et al., 2007; Detrain and Deneubourg, 1997). We show, not surprisingly, that such larger groups are indeed utilized in subsequent cooperative transport phases in *P. longicornis*, as heavier and larger objects correspond to larger groups.

Performance during movement initiation (organization phase)

Paratrechina longicornis porter groups were appropriately sized but were sometimes constrained, especially with small, heavy objects, and we observed variation in mass per ant. On average, groups had a mass per ant of 17.8 mg during movement initiation, but the most extreme trial had a mass per ant of 42.6 mg. This group succeeded even as each ant carried a load 99 times their own weight on average. We hypothesized that trials with heavier loads per porter would have lower performance. This was supported for coordination time, sinuosity and velocity. Heavier objects, per porter, take longer for movement initiation, after which they are moved substantially slower and over somewhat more circuitous paths. While these heavy loads clearly affected the movement process, they did not result in groups failing or even frequently stalling. Even when the ants moved very heavy objects, stalls were so rare that we lacked enough examples for statistical analyses. Both sinuosity and stalls should relate to directional coordination during active movement. Uncoordinated groups may change direction frequently, increasing sinuosity, and should stall more often, perhaps having to re-coordinate during stalls. Just after initiating movement, *P. longicornis* groups perform well in both of these measures; while their sinuosity was affected by challenging objects, it remained fairly low (maximum 2.7), and groups almost never stalled. *Paratrechina longicornis* groups excel at maintaining coordination during initial movement, which agrees with earlier results testing easy-to-carry objects (Gelblum et al., 2015; McCreery et al., 2016b). Our results add that this is true even for heavy, unwieldy objects. It would be interesting to test whether less-coordinated species are more strongly affected by object mass for these measures.

We also hypothesized that object size would impact performance (Table 1). We found it only moderately likely that object size affects sinuosity (combined weight=0.46), and the proportion of time stalled was low across the size range. Sinuosity and stalls, which reflect coordination during movement, do not seem to be strongly affected by object properties. Object size more clearly affected coordination time; for a given mass per ant, groups took longer to begin moving larger objects. This likely relates to group size; larger objects were carried by larger groups. These groups take longer to assemble on the object and to achieve the even distribution that may be required for leverage with large objects (discussed above), leading to high coordination time. Groups carrying larger objects also moved more slowly (lower velocity) than groups carrying smaller objects.

Our results for velocity, that heavier objects per porter and larger objects are each moved more slowly, should be considered in the

context of broader work on the speed of cooperative transport. Consistent with our results, observations of *Pheidologeton diversus* showed that objects requiring larger groups were carried with lower velocity (Moffett, 1988), though the effects of object mass and size were not isolated. In experiments using baits that were uniform or nearly uniform in mass and size (Czaczkes et al., 2011; Gelblum et al., 2015; McCreery et al., 2016b), each found that larger groups (with lower mass per ant) moved at higher speed. This closely aligns with our results for mass per ant (note, however, that our velocity was displacement rather than total distance over time). These earlier experiments did not explore the effect of object size; by doing so, we found that even for a given mass per ant, larger objects (which also corresponded to larger groups) were moved more slowly. While we did not isolate the effects of group size, this agrees qualitatively with earlier work in *Novomessor cockerelli*, in which varying group size while keeping mass per ant constant demonstrated that larger groups move slower because they were constrained by the speed of the slowest porter (Buffin et al., 2018; Wilson et al., 2018).

Performance during obstacle navigation (transport phase)

We also explored how object properties affect transport while groups navigate around a wall-like obstacle (Fig. 1), which directly blocked the groups' nest direction. Obstacle navigation may pose substantially different challenges than initiating movement, in part because the group must decide on a new travel direction when the preferred direction is unavailable. Several other studies have been published on obstacle navigation during cooperative transport by *P. longicornis* (Fonio et al., 2016; Gelblum et al., 2016; McCreery et al., 2016b; Ron et al., 2018), focusing primarily on navigation dynamics and the mechanisms that allow groups to successfully move around complex obstacles. Rather than further examining these mechanisms, we instead focused on how object properties affect the performance of groups as they progress through the obstacle navigation process. We expected these effects to be similar to object effects at the initiation of movement. Our results partially support this. As with movement initiation, groups rarely stalled while navigating around obstacles (1.1% of the time across all trials). The effects of mass per ant during obstacle navigation were similar to those during movement initiation. Groups carrying heavier objects, per porter, took longer to move after hitting the obstacle, and moved more slowly. Sinuosity was moderately affected by mass per ant and size during initiation but was not affected by object properties during obstacle navigation. While groups took more circuitous paths navigating around obstacles than getting started, this was not exacerbated with heavier or larger objects.

However, the effect of object size on velocity during obstacle navigation differed from this effect at movement initiation. Larger objects were moved faster than smaller objects during obstacle navigation, highlighting that these phases pose different challenges. This is not attributable to groups generally speeding up after movement initiation; considering all trials, velocity was slightly lower during obstacle navigation (Fig. 4C), but the effect of size was positive rather than negative. Our evidence for this is equivocal as a model without size performed similarly well, but our results clearly do not support the negative effect we found for movement initiation. *A priori*, we expected such a negative effect; larger objects have larger groups, and one may expect the speed of these groups to be constrained by the slowest porter as found in *N. cockerelli* (Buffin et al., 2018; Wilson et al., 2018), discussed above. We did not isolate group size, but our indirect evidence agrees with this only during movement initiation. During obstacle navigation, object size

seems to have a direct effect that counteracts this, causing the effect of object size to be neutral or positive rather than negative. A possible explanation for this relates to how tightly packed porters are. Ants carrying a small, heavy object will be more crowded, each having a narrow space to grip. This may cause mechanical difficulties; for example, tightly packed groups may hit each other's legs as they walk. Small, heavy objects (with low grip space per mass) were never moved with high velocity (Fig. 5C). While this constraint may be important in both phases, we only found support for larger objects having higher velocities during obstacle navigation. Future work could explore this mechanism directly by manipulating object shape to vary grip space separately from size.

Object size also affected coordination time in contrasting ways in the two transport phases. As coordination time overall was also lower during obstacle navigation, we discuss this in the following section.

Performance across cooperative transport phases

While large objects had higher coordination times than small objects during initial movement, the evidence supports lower coordination time for these objects during obstacle navigation. Furthermore, coordination time overall was substantially lower during obstacle navigation than during movement initiation (Fig. 4A). While it is not necessarily surprising that these two coordination challenges result in differing transport performance and object effects, a detailed consideration of how the challenges differ is worthwhile. To initiate movement, porters must accomplish at least three subtasks: they must (1) grasp the object in an arrangement that allows for transport, (2) lift and/or overcome friction, and (3) reach consensus about travel direction. These tasks interact, but it is useful to consider them separately. A reasonable expectation is that groups navigating around obstacles, perhaps especially those carrying 'difficult' objects, must accomplish these same tasks, as they may need to stop, put down the object and re-organize. But if obstacles do not substantially disrupt coordination, the group may not stop, and thus may not need to re-do tasks 1 and 2. Perhaps the only task these groups must re-do is reaching a new consensus about travel direction (task 3). This task is likely harder when blocked, as the most direct route to the nest is unavailable (McCreery et al., 2016a), but this added difficulty may not outweigh the time saved from being able to maintain coordination without re-organizing. Our 'coordination time' likely measures different things in the two phases, and it may be more appropriate to call it 'directional consensus time' in the context of obstacle navigation. Larger objects have higher coordination time initially, perhaps because they are harder to lift and require a particular arrangement of porters (tasks 1 and 2), but these same objects have lower 'directional consensus time' after encountering obstacles. This is not surprising if they indeed have higher velocity, and if, as we found, groups do not need to stop and re-start. This agrees with earlier work demonstrating that *P. longicornis* porters maintain coordination despite obstacles (Fonio et al., 2016; McCreery et al., 2016b); we found this to be true even when groups carried unwieldy objects that, themselves, posed substantial carrying challenges.

With respect to other performance measures, performance was lower during obstacle navigation than at the start of movement, as we expected. Groups encountering obstacles had lower velocity and less straight paths than immediately after movement began (Fig. 4B,C). This is intuitive, as obstacles put groups in circumstances with no clearly preferred direction. While their performance was lower, *P. longicornis* groups were not substantially disrupted by obstacles, even while carrying difficult objects.

Overall, we demonstrate that *P. longicornis* ants succeed remarkably well at carrying even extremely heavy, unwieldy objects. In part, this is accomplished through size matching of groups to the object at hand. Groups also benefit from not needing to repeat coordination effort – after the initial coordination to begin movement, later decisions about travel direction when moving around obstacles are accomplished rapidly. Transport performance (e.g. coordination time and velocity) is affected by object mass and size mostly as expected, but the nature of these effects varies depending on the phase of transport, especially for object size. Groups maintain comparatively straight paths to the nest regardless of object ‘difficulty’, and almost never stall. Groups carrying heavier objects had lower performance measures throughout the transport process, but some effects of object size, which reduced performance during movement initiation, were absent or reversed during obstacle navigation. The transport ‘difficulty’ of a particular object is not uniform throughout the transport effort. Some objects that groups can begin moving rapidly may be harder to keep moving quickly, and if an object takes a long time to get moving initially, that does not necessarily mean it will be difficult to navigate around obstacles. Thus, if a group struggling to move a large object persists through this initial hurdle, it may be rewarded with an easier trip to the nest. Cooperative transport groups must succeed at both movement initiation and nestward navigation around obstacles while also facing high variation in the objects they carry. The impressive cooperative mechanisms used by *P. longicornis* contend well with this variation, which may partially account for the success of this invasive ant.

Acknowledgements

We thank Tom Getty, Eben Gering and Tomer Czaczkes for valuable discussions, and Tim Szewczyk for input on statistics. Kathleen Kurtenbach extracted data from videos. Stephen Pratt provided the use of his facilities during fieldwork. We thank Ben Green for laser cutting boxes for video stability. We used Justin Werfel's code for data extraction. We thank EBIO's quantitative think tank (QTT) for suggestions on analyses.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: H.F.M., R.N., M.D.B.; Methodology: H.F.M., J.B., R.N., M.D.B.; Software: H.F.M.; Validation: H.F.M.; Formal analysis: H.F.M.; Investigation: H.F.M., J.B.; Resources: H.F.M.; Data curation: H.F.M.; Writing - original draft: H.F.M.; Writing - review & editing: H.F.M., J.B., R.N., M.D.B.; Visualization: H.F.M., R.N., M.D.B.; Supervision: R.N., M.D.B.; Project administration: H.F.M.; Funding acquisition: H.F.M.

Funding

This work was funded in part by the University of Colorado Graduate School and Department of Ecology and Evolutionary Biology. H.F.M. is supported by a James S. McDonnell Foundation Postdoctoral Fellowship Award in Studying Complex Systems.

Data availability

Data and code used to produce figures and conduct statistical analyses are publicly available from figshare (McCreery et al., 2019): doi:10.6084/m9.figshare.8969834

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.206821.supplemental>

References

- Berman, S., Lindsey, Q., Sakar, M. S., Kumar, V. and Pratt, S. C. (2011). Experimental study and modeling of group retrieval in ants as an approach to collective transport in swarm robotic systems. *Proc. IEEE* **99**, 1470–1481. doi:10.1109/JPROC.2011.2111450
- Buffin, A. and Pratt, S. C. (2016). Cooperative transport by the ant *Novomessor cockerelli*. *Insect. Soc.* **63**, 429–438. doi:10.1007/s00040-016-0486-y
- Buffin, A., Sasaki, T. and Pratt, S. C. (2018). Scaling of speed with group size in cooperative transport by the ant *Novomessor cockerelli*. *PLoS ONE* **13**, e0205400. doi:10.1371/journal.pone.0205400
- Cerdá, X., Angulo, E., Boulay, R. and Lenoir, A. (2009). Individual and collective foraging decisions: a field study of worker recruitment in the gypsy ant *Aphaenogaster senilis*. *Behav. Ecol. Sociobiol.* **63**, 551–562. doi:10.1007/s00265-008-0690-5
- Cogni, R. and Oliveira, P. S. (2004). Recruitment behavior during foraging in the neotropical ant *Gnamptogenys moelleri* (Formicidae: Ponerinae): Does the type of food matter? *J. Insect Behav.* **17**, 443–458. doi:10.1023/B:JOIR.0000042534.95716.7a
- Czaczkes, T. J. and Ratnieks, F. L. W. (2012). Pheromone trails in the Brazilian ant *Pheidole oxyops*: extreme properties and dual recruitment action. *Behav. Ecol. Sociobiol.* **66**, 1149–1156. doi:10.1007/s00265-012-1367-7
- Czaczkes, T. J. and Ratnieks, F. L. W. (2013). Cooperative transport in ants (Hymenoptera: Formicidae) and elsewhere. *Myrmecol. News* **18**, 1–11.
- Czaczkes, T. J., Nouvellet, P. and Ratnieks, F. L. W. (2011). Cooperative food transport in the Neotropical ant, *Pheidole oxyops*. *Insectes Soc.* **58**, 153–161. doi:10.1007/s00040-010-0130-1
- Daly-Schweitzer, S., Beugnon, G. and Lachaud, J.-P. (2007). Prey weight and overwhelming difficulty impact the choice of retrieval strategy in the Neotropical ant *Gnamptogenys sulcata* (F. Smith). *Insectes Soc.* **54**, 319–328. doi:10.1007/s00040-007-0949-2
- Detrain, C. and Deneubourg, J.-L. (1997). Scavenging by *Pheidole pallidula*: a key for understanding decision-making systems in ants. *Anim. Behav.* **53**, 537–547. doi:10.1006/anbe.1996.0305
- Feinerman, O., Pinkoviezky, I., Gelblum, A., Fonio, E. and Gov, N. S. (2018). The physics of cooperative transport in groups of ants. *Nat. Phys.* **14**, 683–693. doi:10.1038/s41567-018-0107-y
- Fonio, E., Heyman, Y., Boczkowski, L., Gelblum, A., Kosowski, A., Korman, A. and Feinerman, O. (2016). A locally-blazed ant trail achieves efficient collective navigation despite limited information. *eLife* **5**, e20185. doi:10.7554/eLife.20185
- Franks, N. R. (1986). Teams in social insects: group retrieval of prey by army ants (*Eciton burchelli*, Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **18**, 425–429. doi:10.1007/BF00300517
- Franks, N. R., Sendova-Franks, A. B., Simmons, J. and Mogie, M. (1999). Convergent evolution, super-efficient teams and tempo in Old and New World army ants. *Proc. Biol. Sci.* **266**, 1697–1701. doi:10.1098/rspb.1999.0834
- Franks, N. R., Sendova-Franks, A. B. and Anderson, C. (2001). Division of labour within teams of New World and Old World army ants. *Anim. Behav.* **62**, 635–642. doi:10.1006/anbe.2001.1794
- Gelblum, A., Pinkoviezky, I., Fonio, E., Ghosh, A., Gov, N. and Feinerman, O. (2015). Ant groups optimally amplify the effect of transiently informed individuals. *Nat. Commun.* **6**, 7729. doi:10.1038/ncomms8729
- Gelblum, A., Pinkoviezky, I., Fonio, E., Gov, N. S. and Feinerman, O. (2016). Emergent oscillations assist obstacle negotiation during ant cooperative transport. *Proc. Natl. Acad. Sci. USA* **113**, 14615–14620. doi:10.1073/pnas.1611509113
- Hölldobler, B. and Wilson, E. O. (1990). *The Ants*, 1st edn. Belknap Press of Harvard University Press.
- Kumar, G. P., Buffin, A., Pavlic, T. P., Pratt, S. C. and Berman, S. M. (2013). A stochastic hybrid system model of collective transport in the desert ant *Aphaenogaster cockerelli*. In Proceedings of the 16th international conference on hybrid systems: computation and control, pp. 119–124. New York, NY, USA: ACM.
- Lukacs, P. M., Burnham, K. P. and Anderson, D. R. (2010). Model selection bias and Freedman's paradox. *Ann. Inst. Stat. Math.* **62**, 117. doi:10.1007/s10463-009-0234-4
- McCreery, H. F. (2017). A comparative approach to cooperative transport in ants: individual persistence correlates with group coordination. *Insect. Soc.* **64**, 535–547. doi:10.1007/s00040-017-0575-6
- McCreery, H. F. and Breed, M. D. (2014). Cooperative transport in ants: a review of proximate mechanisms. *Insectes Soc.* **61**, 99–110. doi:10.1007/s00040-013-0333-3
- McCreery, H. F., Correll, N., Breed, M. D. and Flaxman, S. (2016a). Consensus or deadlock? Consequences of simple behavioral rules for coordination in group decisions. *PLoS ONE* **11**, e0162768. doi:10.1371/journal.pone.0162768
- McCreery, H. F., Dix, Z. A., Breed, M. D. and Nagpal, R. (2016b). Collective strategy for obstacle navigation during cooperative transport by ants. *J. Exp. Biol.* **219**, 3366–3375. doi:10.1242/jeb.143818
- McCreery, H. F., Bilek, J., Nagpal, R. and Breed, M. D. (2019). Data & Code for “Effects of load mass and size on cooperative transport in ants over multiple transport challenges.” *figshare*. <http://dx.doi.org/10.6084/m9.figshare.8969834>
- Moffett, M. (1988). Cooperative food transport by an Asiatic ant. *Nat. Geograph. Res.* **4**, 386–394.
- Robson, S. K. and Traniello, J. F. A. (1998). Resource assessment, recruitment behavior, and organization of cooperative prey retrieval in the ant *Formica schaufussi* (Hymenoptera: Formicidae) RID D-1168-2011. *J. Insect Behav.* **11**, 1–22. doi:10.1023/A:1020859531179

- Robson, S. K. and Traniello, J. F.** (2002). Transient division of labor and behavioral specialization in the ant *Formica schaufussi*. *Naturwissenschaften* **89**, 128-131. doi:10.1007/s00114-002-0300-8
- Ron, J. E., Pinkoviezky, I., Fonio, E., Feinerman, O. and Gov, N. S.** (2018). Bi-stability in cooperative transport by ants in the presence of obstacles. *PLoS Comput. Biol.* **14**, e1006068. doi:10.1371/journal.pcbi.1006068
- Symonds, M. R. E. and Moussalli, A.** (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* **65**, 13-21. doi:10.1007/s00265-010-1037-6
- Traniello, J. F. A. and Beshers, S. N.** (1991). Maximization of foraging efficiency and resource defense by group retrieval in the ant *Formica schaufussi*. *Behav. Ecol. Sociobiol.* **29**, 283-289. doi:10.1007/BF00163986
- Wetterer, J. K.** (2008). Worldwide spread of the longhorn crazy ant, *Paratrechina longicornis* (Hymenoptera: Formicidae). *Myrmecolog. News* **11**, 137-149.
- Wetterer, J. K., Miller, S. E., Wheeler, D. E., Olson, C. A., Polhemus, D. A., Pitts, M., Ashton, I. W., Himler, A. G., Yospin, M. M., Helms, K. R. et al.** (1999). Ecological dominance by *Paratrechina longicornis* (Hymenoptera: Formicidae), an invasive tramp ant, in biosphere 2. *Fla. Entomol.* **82**, 381-388. doi:10.2307/3496865
- Wilson, S., Buffin, A., Pratt, S. C. and Berman, S.** (2018). Multi-robot replication of ant collective towing behaviours. *Open Sci.* **5**, 180409. doi:10.1098/rsos.180409
- Wojtusiak, J., Godzińska, E. and Dejean, A.** (1995). Capture and retrieval of very large prey by workers of the African weaver ant, *Oecophylla longinoda* (Latreille 1802). *Trop. Zool.* **8**, 309-318. doi:10.1080/03946975.1995.10539287