

A comparative approach to cooperative transport in ants: individual persistence correlates with group coordination

H. F. McCreery¹ 

Received: 22 March 2017 / Revised: 20 June 2017 / Accepted: 10 July 2017 / Published online: 20 July 2017
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Abstract When groups of ants work together to carry large objects—called cooperative transport—they must form consensus on a travel direction. In many species, groups are unsuccessful at this decision, and deadlock. In other collective decisions, including nest-site selection in honeybees, individuals' enthusiasm or recruitment intensity for a given option affects the selection process. A similar mechanism may be important during cooperative transport in ants and may account for coordination differences among species. Results from theoretical models suggest that individuals' *persistence*—their reluctance to give up or change their preferred direction—may promote coordination. More persistent individuals formed more successful groups in a theoretical context. As an empirical test of this hypothesis, I examined cooperative transport in four ant species that differ substantially in their group-level coordination, from exceedingly coordinated to rarely successful. I focused on the beginning of transport, evaluating groups' transitions from uncoordinated to successful. I measured two types of persistence at the individual level—total engagement effort and local engagement time—and I measured group coordination for each species. In one species, I also manipulated persistence by adding a force equivalent to infinitely persistent ants to the existing transport groups. Species with more persistent individuals succeeded more often and

formed more coordinated transport groups, with more direct paths. Furthermore, adding two infinitely persistent ants to the existing groups seemed to moderately increase their path directness. These results support the hypothesis that high individual persistence promotes group coordination during cooperative transport, and this study informs the mechanisms of emergent coordination.

Keywords Cooperative transport · Persistence · Collective decision · Formicidae · Emergent behavior · Collective behavior

Introduction

Ant colonies exhibit some of the most impressive coordination in nature, making them excellent models for cooperation in animal groups. Ants cooperate to construct nests, care for brood, forage, and more. These are emergent group behaviors (Fewell 2015); groups accomplish tasks well beyond the capabilities of individuals, and individual ants generally act autonomously, based on local information (Camazine et al. 2001; Fewell 2015). A conspicuous example of ant coordination is cooperative transport, which occurs when groups of ants work together to move a large object to the colony's nest (Moffett 1992; Berman et al. 2011; Czaczkes and Ratnieks 2013; McCreery and Breed 2014). Ant species vary widely in group transport ability. For example, longhorn crazy ants, *Paratrechina longicornis*, jointly navigate maze-like obstacles while maintaining coordination (McCreery et al. 2016b), while many species are uncoordinated and rarely succeed, with transport attempts characterized by many deadlocks (Moffett 2010; Czaczkes and Ratnieks 2013). Individuals in deadlocked groups may have arrived at the object from different paths,

Electronic supplementary material The online version of this article (doi:10.1007/s00040-017-0575-6) contains supplementary material, which is available to authorized users.

✉ H. F. McCreery
helen.mccreery@colorado.edu

¹ Department of Ecology and Evolutionary Biology, University of Colorado, Ramaley N122, Campus Box 334, Boulder, CO 80309-0334, USA

may have differing information about nest location, or individuals may deadlock for other reasons. Effective cooperative transport requires that groups break any deadlocks that occur, and form consensus with respect to travel direction. This consensus decision is difficult for many species.

Consensus decisions are well studied in some other contexts, particularly in nest-site selection in honeybees and *Temnothorax* ants (Mallon et al. 2001; Pratt et al. 2002; Visscher 2007; Seeley 2010; Seeley et al. 2012). During these decisions, workers advertise for particular nest options until a quorum is reached. Importantly, individuals advertise with higher probability or more intensely for higher quality options (Pratt and Sumpter 2006; Visscher 2007; Robinson et al. 2009), and may attempt to prevent other workers from advertising for different options (Niven 2012; Seeley et al. 2012; Pais et al. 2013). Thus, individuals' enthusiasm for their favored option affects the mechanics of colonies choosing a single nest site.

Is there an analogous mechanism that affects coordination during cooperative transport in ants? Individual workers may each have a favored direction, and their enthusiasm for and fidelity to that direction—or their persistence—may affect a group's ability to form and maintain consensus (McCreery and Breed 2014). Indeed, recent theoretical work identified persistence as an important trait that may affect coordination in cooperative transport (McCreery et al. 2016a). Persistence describes how long an individual continues attempting to move an object in the same direction if transport is unsuccessful (McCreery and Breed 2014). While ants may have many potential sources of information about nest direction, such as phomonal or visual cues, and path integration (e.g. Cheng et al. 2014; Fonio et al. 2016), persistence describes what individuals do with that information. An individual with high persistence will not deviate from their assessment of nest direction even when unsuccessful. Because ant species vary widely in cooperative transport ability, this task provides a natural system to compare behavioral traits in coordinated and uncoordinated transporters and so to understand how persistence contributes to coordination. Studies on consensus decisions have rarely made quantitative comparisons among species or groups that vary in their decision abilities, and as far as I know, such a study has never been conducted in the context of cooperative transport. By measuring persistence in individuals and coordination in groups that vary in ability, I directly examine the putative mechanisms of emergent behavior.

One may expect groups with high mean persistence to be relatively uncoordinated (persistence decreases coordination), because individuals may pull in opposing directions for a long time (McCreery and Breed 2014). On the other hand, a group made up of individuals with low persistence

may fail to form consensus, because individuals change directions too frequently, so it may also be reasonable to expect persistence to promote coordination. McCreery et al. (2016a) explored these opposing ideas by testing the consequences of persistence for coordination in a theoretical context, and found that high individual persistence promoted group coordination in most cases. Intuitively, I also expect variation in persistence within groups to be important (McCreery and Breed 2014). If a small number of group members are highly persistent, while others readily change direction, the less persistent individuals may rapidly converge on the direction favored by the persistent individuals. This hypothesis has been supported in the context of navigation during successful cooperative transport (Gelblum et al. 2015), but has not previously been tested—nor has the effect of persistence in general been empirically evaluated—for initial collective decisions about travel direction. McCreery et al. (2016a) defined persistence as individuals' resistance to giving up or to changing the direction which they are trying to move the object. It may be useful to consider persistence at different scales—individuals may quickly “give up” altogether, or may temporarily give up, only to re-engage in a new direction. One expects these behaviors to have different impacts for coordination. Thus, I define two types of persistence: total engagement effort—how long individuals spend attempting to move an object regardless of direction—and local engagement time—how long a particular “bout” of engagement lasts, where a bout is a consistent pull in a particular direction. These measures are described further below.

Measuring group coordination—the extent to which individuals are aligned with respect to travel direction—is central to understanding emergent cooperation during transport efforts, including effects of persistence. Here, I used two coordination measures: sinuosity, which is the ratio of the total path length of the group to the displacement, and the proportion of transport attempts that were successful (success fraction). These efficiency measures provide information about the extent of coordination among individuals. These measures are also well suited for use in comparing coordination across species, as they are not strongly affected by other differences in species or environments, such as walking speed or food availability. Low sinuosity indicates a highly direct path, and higher coordination. I refer to path “directness,” below, as well as to sinuosity; these are inverse measures.

I evaluate how persistence—i.e., total engagement effort and local engagement time—affects cooperative transport success and sinuosity. Based on theoretical results, I hypothesize that high persistence increases coordination (McCreery et al. 2016a), resulting in more frequent success and lower (more direct) sinuosity. I focus on the beginning of the transport process, evaluating how groups move from a

pre-success, uncoordinated period to successful movement. Therefore, I also measure individual persistence in an unsuccessful scenario: with immovable bait. By measuring individual behavioral traits and their effect on group success and sinuosity, I aim to directly explore the mechanisms of emergent behavior. I focused on the following three questions. (1) *How do total engagement effort and local engagement time differ among species?* (2) *Are species with higher total engagement effort and local engagement time more successful and/or direct?* (3) *Does changing the behavioral makeup of groups improve sinuosity?* I conducted two studies. In Study 1, I measured total engagement effort and local engagement time, and I separately measured success fraction and sinuosity in four species to explore questions 1 and 2. In Study 2, I changed the behavioral makeup of cooperative transport groups in one species to alter total engagement effort and local engagement time, observing how these changes affected sinuosity.

Materials and methods

Study system

In Study 1, I observed four ant species in the ant subfamily Formicinae, including *Paratrechina longicornis* and the following three *Formica* species that represent different species groups within the genus: *F. obscuripes* (rufa species group), *F. pallidefulva* (pallidefulva species group), and *F. podzolica* (fusca species group). Study 2 was conducted in 2012 and focused on *F. podzolica* only, because this species typically succeeds at cooperative transport, but with relatively high (poor) sinuosity. I chose these four species, because, anecdotally, they vary widely in transport efficiency, from extremely efficient (*P. longicornis*, Gelblum et al. 2015; McCreery et al. 2016b) to largely unsuccessful (*F. pallidefulva*), with *F. obscuripes* and *F. podzolica* being moderately successful, as shown in the movie (Online Resource 1). I conducted experiments on *F. obscuripes*, *F. pallidefulva*, and *F. podzolica* in 2012 and 2013 at several sites in Boulder County, Colorado, and on *P. longicornis* in 2014 at Arizona State University in Tempe, Arizona and at Biosphere 2 in Oracle, Arizona.

F. pallidefulva colonies are found in a variety of habitats in the eastern United States and southeastern Canada. Its range extends west to lower elevation areas in the Rocky Mountains (Trager et al. 2007). The population at my study site builds underground nests with cryptic entrances and has workers approximately 4–5 mm long. *F. obscuripes* is found in a broad range of habitats, including at high elevation (Gregg 1963). They build thatch nests from conifer needles and have workers that are approximately 6 mm long (Gregg 1963). *F. podzolica* lives mostly in boreal coniferous forests

(Francoeur 1973) and is common at high elevations. Worker ants are polymorphic, ranging continuously in size with most workers being approximately 4 mm long. *F. podzolica* build large mounds in which they nest, and have large, polygynous colonies (Francoeur 1973). *P. longicornis* are widely distributed tropical and subtropical “tramp ants,” especially common in disturbed and urban environments (Wetterer 2008). *P. longicornis* are approximately 3 mm long, and are invasive in Arizona, where I studied them.

I conducted observations on a total of 18 colonies in the four species. In the case of *F. pallidefulva*, I only used one colony, because several identified colonies were destroyed by construction crews. Because I conducted fieldwork over multiple years, I was not able to get all measurements for all colonies, so I analyzed data at the species, rather than colony, level. Details of the number of colonies and individuals for each study are included in Table 1. Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.45nr3>.

Study 1: cross-species comparisons

I hypothesized that high individual persistence promotes group coordination, and that high variation in persistence may also promote coordination. A trait related to persistence is conformity, which has previously been evaluated for *P. longicornis* in transport groups that were already coordinated and moving successfully. Conformity—the extent to which workers are guided by directions imposed by a minority—seems to be important for maintaining a correct transport direction in this species (Gelblum et al. 2015). Joining and leaving rates of progressing transport attempts have also been evaluated in some species (Czaczkes et al. 2011; Buffin and Pratt 2016). Yet, it remains unknown whether individuals’ readiness to change behavior affects group coordination, especially during the initial decision on travel direction. Groups only begin moving successfully after sufficient consensus has been reached; therefore, it is valuable to measure persistence when the group is unsuccessful. Study 1 consisted of two experiments to see how individual persistence affects the ability of groups to choose a travel direction. In the first experiment, I measured two types of persistence in each of the four study species: total engagement effort and local engagement time. In the second, I recorded two measures of coordination, success fraction and sinuosity, in each species.

To characterize how the individual traits total engagement effort and local engagement time differ within and among species (question 1), and to see whether these traits are correlated with group-level efficiency (question 2), I measured each of these traits in *F. obscuripes*, *F. pallidefulva*, *F. podzolica*, and *P. longicornis*. For all measures, I first placed white paper or a foam board with paper affixed

Table 1 Data structure information and mean worker mass and bait mass for each species

Species	Mean worker mass (mg)	Study 1				Study 2				
		Persistence measures (individual)	Coordination measures (group)			Force measures	Bait mass	Sinuosity before/after adding artificial ants		
			Sample size (# of colonies)	Sinuosity sample size (# of colonies)	# of attempts recorded			Mean bait mass (range)	Sample size (# of colonies)	Mean (range)
<i>P. longicornis</i>	0.43	45 (5)	14 (4)	39	0.11 g (0.080–0.18)	–	–	–	–	–
<i>F. podzolica</i>	3.4	41 (2)	15 (6)	47	0.90 g (0.57–1.15)	47 (10)	1.05 g (0.86–1.18)	45 (10)	42 (10)	16 (6)
<i>F. obscuripes</i>	5.2	42 (4)	11 (2)	25	1.24 g (0.95–2.03)	–	–	–	–	–
<i>F. pallidefulva</i>	2.8	33 (1)	9 (1)	30	1.47 g (1.00–1.86)	–	–	–	–	–

to it on relatively flat ground near colony entrances. I used foam when it was necessary to smooth the surface, and paper when conducting trials on pavement that was already smooth. To avoid potential effects of non-nestmate pheromone trails persisting on the board, I replaced the paper when moving between colonies. When using a foam board, I used soil, sand, and twigs surrounding the board to make it as flush with the ground as possible.

Total engagement effort and local engagement time

These two individual measures of persistence provide information on different scales. I measured total engagement effort as the proportion of time a worker was near the object that they actively attempted to move the object; this is a measure of overall enthusiasm. Local engagement time, on the other hand, is measured at a smaller temporal scale, and is the average length of pulling bouts. A pulling bout begins when a worker begins attempting to move the object, and ends either if they stop pulling—even temporarily, perhaps moving to a new gripping point—or if they substantially change the direction of attempted movement without stopping. Local engagement time, therefore, incorporates an individual's fidelity to their chosen direction.

I recorded the persistence of individuals in an unsuccessful scenario to characterize behavior before successful movement occurs. To ensure that the ants were unsuccessful, I measured total engagement effort and local engagement time, while workers attempted to move bait that was pinned down. I pinned dead house crickets (*Acheta domestica*) to the trial surface (paper or foam) and video recorded ants' attempts to transport them (example video shown in Online Resource 2). I allowed ants to recruit naturally to the cricket. Because the crickets

were pinned down, these attempts were never successful. For each individual, the length and number of pulling bouts were recorded in JWatcher. Pulling bouts began when individuals began attempting to move the cricket, and each bout ended either when the worker stopped pulling for at least 1 s, or when the worker changed the direction of attempted movement. These two conditions often occurred simultaneously, as individuals moved to a new gripping point on the cricket. My measure of total engagement effort was the worker's total time spent pulling divided by the amount of time that individual was recorded. While this measure can be affected by the size of the video frame, which I did not strictly standardize, possible effects of frame-size were likely small, as ants tended to either remain close to the object or leave altogether. My measure of local engagement time was the average length pulling bouts. Crickets were obtained from a local pet store and killed by freezing. Individual crickets were reused between trials but not between colonies to limit possible cross-colony pheromone interactions. Sample sizes for persistence measurements for each species are shown in Table 1.

Coordination

To compare transport coordination among species, it is important to choose measures that are not affected by species or colony traits unrelated to coordination, such as walking speed, worker strength, or colony size. To isolate coordination from other factors affecting the delivery of food to nests, I used success fraction and sinuosity—the ratio of the total path length of the group to the displacement (McCreery and Breed 2014; Buffin and Pratt 2016). Groups with poor coordination about travel direction are likely to change direction frequently, indicated by high sinuosity.

These measures of coordination are particularly well suited for use in comparing coordination across species.

I measured the sinuosity of groups by placing large baits on paper or foam boards next to colonies and video recording cooperative transport attempts (example video shown in Online Resource 3). I allowed ants to recruit naturally to the baits. I did not follow transport attempts all the way back to nests, instead measuring sinuosity in the initial period of transport captured on video. Each trial for sinuosity ended when the group left the video frame. Sinuosity does not entirely capture coordination; as an additional measure of coordination; I observed the proportion of transport attempts in which groups displaced at least 10 cm (success fraction). I considered groups moving a displacement distance of at least 10 cm to be “successful” at coordinating whether or not they completed their journey to their nest. Trials in which there were an insufficient number of ants actively trying to move the bait—based on observed movements—were not counted as attempts. For example, if I observed that a given bait mass was not moved by fewer than three ants, I did not count as attempts trials in which only two ants were consistently present. To maximize sample sizes for sinuosity, in one trial, I recorded sinuosity for a group that moved substantially but were ultimately unsuccessful (displaced less than 10 cm total). Sinuosity and proportion of attempts that succeeded are efficiency measures that provide information about extent of coordination among individuals.

For each species, I used baits too heavy for a single individual to move, but not so heavy that cooperative transport was prohibitively difficult. Because the four species vary in morphology, including mass and strength, the desired mass of baits varied among the species as shown in Table 1. I obtained mean mass estimates to confirm that our bait masses were reasonable, by weighing between 20 and more than 100 workers of each species, killed by freezing (Table 1). It was necessary to weigh many more *P. longicornis* workers than the other species, as this species has low mass and a large number was needed to register on the scale. Bait masses were not strictly proportional to worker mass, because mass is only one of many factors that may affect moving strength. For example, *F. pallidefulva* workers are lighter than *F. obscuripes* workers, but I found that I needed to make baits for *F. pallidefulva* at least as heavy as those for *F. obscuripes*, because *F. pallidefulva* workers were consistently able to pull lighter ones individually. Baits for all species consisted of pieces of dead insects or entire large dead insects. To consistently make baits that were heavy enough for *F. obscuripes*, *F. pallidefulva*, and *F. podzolica*, I constructed baits of multiple dead insects lanced onto the same pin, sometimes with small pieces of metal added for additional mass. All baits were highly attractive to workers, and elicited transport attempts from workers in all trials. As

with the persistence measurements, baits and trial surface (paper) used for measuring success fraction and sinuosity were reused for multiple trials within a colony, but not across colonies. While in later trials, it is possible that more workers had been recruited to the bait, I did not observe substantial variation between early and late trials, and my coordination measures are independent of recruitment rate. Sample sizes for all measurements are included in Table 1. I measured sinuosity for a subset of successful attempts recorded. For *F. podzolica*, I measured sinuosity from some control trials from Study 2. In the case of *F. pallidefulva*, my sample size for sinuosity was constrained by having a smaller number of successful attempts, as I could not extract these measurements for failed attempts and this species did not often succeed.

To extract trajectory data from videos, the location of carried baits was manually recorded every second using MATLAB. This provides the trajectory of the group rather than of individual ants. I then used trajectories to calculate sinuosity: the ratio of path length to displacement.

Study 2: persistence manipulation

To explore whether altering persistence affects sinuosity, or path directness (question 3), I manipulated the persistence structure of *F. podzolica* transport groups by adding artificial ants to transport efforts already in progress. These artificial ants mimicked the pulling force of *F. podzolica* workers and were infinitely persistent, pulling counter to the previous group movement, as described below. Their addition increased both the mean and the variation in the transport group of both types of persistence: total engagement effort and local engagement time. For each trial, I measured the sinuosity of the transport effort both before and after adding artificial ants.

Force measurement

I first measured a maximum force these workers apply to objects they attempt to carry. I induced workers, individually, to pull on a light chain coiled on a foam board with paper as described above (Fig. 1a). I used a spirit level to ensure that the board was as level with the ground as possible. I did not need to attach bait to the chain, as *F. podzolica* workers naturally, consistently, and enthusiastically pulled on the plain metal chain (example video shown in Online Resource 4). However, I dipped the end of the chain into tuna packed in oil, so that workers preferentially grasped the end of the chain rather than another part. As workers pulled on the coiled chain, they were required to move an increasingly longer, and heavier, length of chain. I measured the length of chain each ant pulled before giving up or changing direction and calculated the corresponding

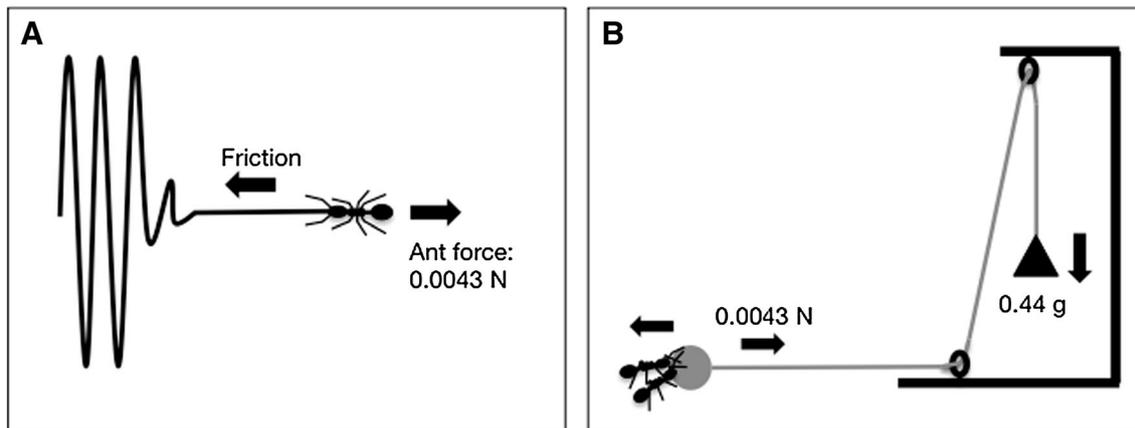


Fig. 1 Experimental setup for Experiment 2. *Left panel* Force was measured by inducing workers, individually, to pull on a coiled chain. As workers moved the chain the weight of chain they were moving gradually increased until they gave up. *Right panel* Ants were

mass that the worker successfully moved. I used a brush to remove other ants from the foam board, so that only a single ant pulled on the chain at a time.

To calculate pulling force from the weight of chain pulled, I measured the coefficient of friction between the chain and the board. I did this by gradually tilting the board until the chain began to slip. I used the angle at which the chain slipped to calculate the coefficient of static friction between the chain and the board. The static coefficient is appropriate, because workers frequently start and stop pulling rather than continuously pull (see video in Online Resource 1). I used the coefficient of friction and the weight of chain each worker successfully moved to calculate the force that worker had applied to the chain before giving up. I measured the force of a total of 47 workers from 10 colonies. I took the mean of this force within each colony, and averaged those colony means to find the grand mean for *F. podzolica* workers, which determined the weight which I added for the artificial ants described above. This colony-level mean force (0.0043 N) differed from the grand mean—pooling data from all colonies—by only 2%.

Study 2 details

I induced cooperative transport by placing a heavy bait, which was attached to a string, on a foam board covered with paper and replaced between colonies as described above. After a group of ants had moved the bait at least 5 cm, I added one or more artificial ants by adding weight (small beads in a paper basket) on the end of the string; thus applying a constant force of the magnitude corresponding to the force typically applied by a worker (Fig. 1b). I added twice this force to simulate two infinitely persistent ants attempting to move the object in the same direction, and for a control group, no force was applied to the object being

simulated by adding weight, corresponding to the force typically applied by workers, on the end of the string as shown. Force and weight shown are for the treatment simulating one artificial ant—twice this weight was added to simulate two ants

transported. The total length of the string was approximately 1 m. The distance groups could move the object was constrained by the height of my apparatus: the object could be displaced 40 cm away from the apparatus before running out of string. I discarded any trials during which this occurred. The direction of the added force was different from the overall direction of movement. I set up the apparatus, determining the direction of added force, before each trial began. Therefore, I could not truly standardize the direction of pulling with respect to the direction of movement of the ant group. I set up the apparatus, such that if the ants moved in the direction of the nest—which did not always occur—the added force would be in the opposite direction. If a group of ants' prevailing movement was such that my added force would be pulling in the same direction, I either moved the apparatus or discarded the trial. I protected my apparatus from wind to keep the force on the bait constant. The weight added to the string was not enough to move the bait without the contributions of real ants. I completed five trials of each treatment (control, one, and two artificial ants), at each of ten *F. podzolica* colonies. However, I excluded trials in which the combined effect of wind and the artificial ant(s) was enough to drag the bait. An example trial is shown in Online Resource 4. I extracted bait trajectory data from the videos manually, as described above for sinuosity measurements for Study 1.

Statistical analyses

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

Question 1: How do total engagement effort and local engagement time differ among species? I compared the individual-level traits, total engagement effort, and local engagement time among species using analysis of variance

(ANOVA), on log-transformed data. For both total engagement effort and local engagement time, log-transformed data fit the assumption of normality. I used Tukey's post hoc comparisons to compare species pairs. To see whether total engagement effort and local engagement time were significantly correlated among individuals, I used Pearson product-moment correlation tests on log-transformed data, within each species and with data pooled across species.

Question 2: Are species with higher total engagement effort and local engagement time more successful and/or direct? I first characterized how species differed in my coordination measures. I used a Pearson's χ^2 test (contingency test) to evaluate differences among species in the proportion of cooperative transport attempts that were successful. Sinuosity data could not be transformed to meet assumptions of parametric tests, so I compared sinuosity among species with a Kruskal–Wallis rank sum test, using Dunn post hoc comparisons with a Bonferroni adjustment to compare species pairs.

Because total engagement effort and local engagement time are individual measures, and transport efficiency is measured at the group level, I do not have matched persistence and efficiency data—e.g., there is no efficiency information for a particular individual for whom I have persistence data, because efficiency can only be measured at the group level. Furthermore, because these were field experiments at large colonies occurring over multiple years, I could not measure persistence of individuals from groups for which I had efficiency data. I am unable to pair my individual- and group-level measures for statistical analysis. Therefore, to look at correlations between individual and group traits, I pooled measurements at the species level, performing correlations on mean persistence and coordination values for each species. I conducted Kendall's rank correlation tests on all combinations of total engagement effort or local engagement time with either sinuosity or success fraction; thus, there are four points per correlation test, each corresponding with one of the four species.

Question 3: Does changing the behavioral makeup of groups affect sinuosity? I compared sinuosity in groups before and after adding infinitely persistent artificial ants, conducting separate tests for each treatment group. As sinuosity data could not be transformed to meet assumptions of parametric tests, I used Wilcoxon's signed rank tests for these paired comparisons.

Results

How do total engagement effort and local engagement time differ among species?

Paratrechina longicornis workers had the highest total engagement effort and local engagement time (Fig. 2,

Table 2). *F. podzolica* and *F. obscuripes* both had moderate values, with *F. podzolica* having slightly higher mean total engagement effort and slightly lower mean local engagement time than *F. obscuripes*. *F. pallidefulva* workers had the lowest measurements for both traits. There were significant differences among species both for total engagement effort ($F = 43.18$, $p < 0.0001$), and local engagement time ($F = 22.25$, $p < 0.0001$). Furthermore, Tukey's post hoc comparisons indicate that all species significantly differ from all others for both measures, except *F. podzolica* and *F. obscuripes* did not differ in local engagement time, and *F. pallidefulva* and *F. obscuripes* only marginally differed in total engagement effort ($p = 0.051$). Complete results of post hoc comparisons are included in a table (Online Resource 5). Qualitatively, I found that *P. longicornis* workers had the largest variation in persistence measures in addition to being the most persistent (Figs. 2, 3). This was true for both total engagement effort and local engagement time, and one *P. longicornis* attempted to pull a pinned cricket consistently in the same direction for more than 90 s, which is more than ten times the mean across individuals. In summary, for both measures of persistence, *P. longicornis* workers were the most persistent, *F. obscuripes* and *F. podzolica* were moderately persistent, and *F. pallidefulva* workers were the least persistent.

Total engagement effort and local engagement time were correlated; individuals with high total engagement effort tended to have high local engagement time (Pearson's $r = 0.69$, $p < 0.0001$, Fig. 3). This correlation was significant within each species as well as for the pooled data (*P. longicornis*: $r = 0.68$, $p < 0.0001$; *F. podzolica*: $r = 0.65$, $p < 0.0001$; *F. obscuripes*: $r = 0.54$, $p = 0.0002$; *F. pallidefulva*: $r = 0.56$, $p = 0.0007$).

Are species with higher total engagement effort and local engagement time more successful and/or direct?

I evaluated cooperative transport coordination with two measures: the proportion of transport attempts that were successful—moving at least 10 cm given that enough ants were present—and sinuosity of successful transports. *P. longicornis* groups were the most coordinated: nearly every attempt was successful (97.4%), and transport efforts had low sinuosity, moving essentially in straight lines (Table 3; Fig. 4, Online Resource 1). Groups of *F. podzolica* workers were also successful in nearly all attempts (95.7%), but their transport attempts had higher sinuosity, on average covering over twice the distance they needed to. The efficiency of *F. obscuripes* groups was similar to *F. podzolica* groups, although these groups were somewhat less successful than *F. podzolica* (88% of attempts). Finally, groups of *F.*

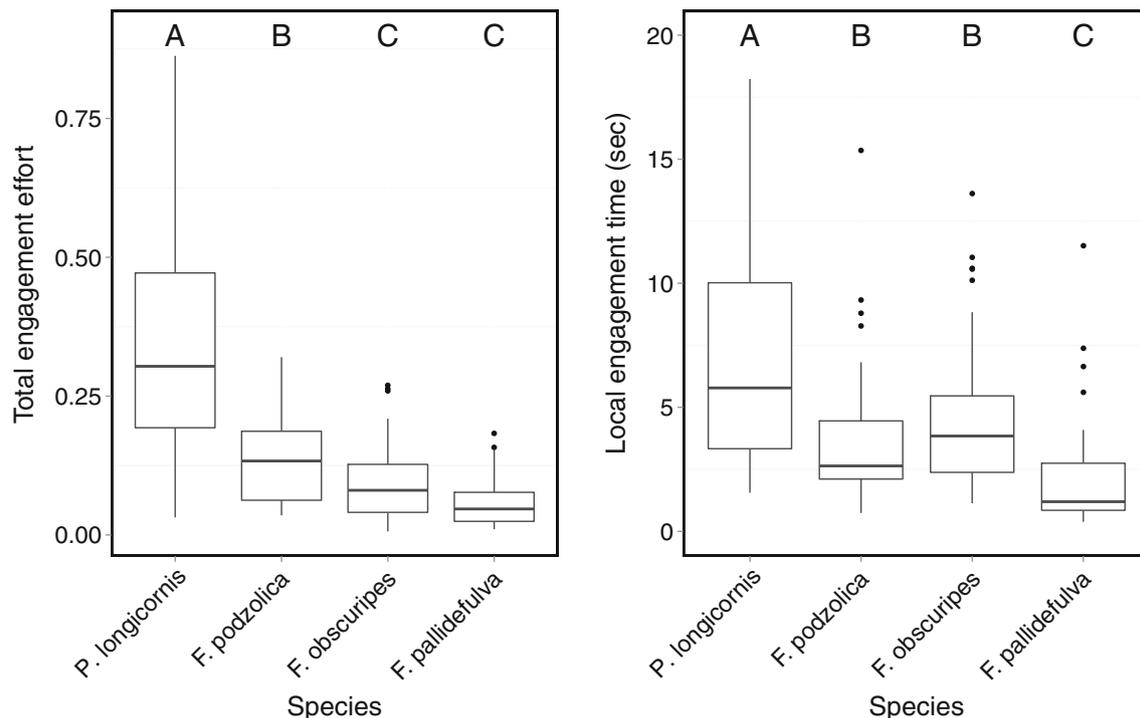


Fig. 2 Individual measures of persistence. Letters indicate significant differences, from Tukey's post hoc comparisons. *Left panel* Total engagement effort for each species, measured on individuals (species significantly differ: $F = 43.18$, $p < 0.0001$). Total engagement effort is the proportion of time that an individual was in the video frame that the individual was actively trying to move the cricket. *Right panel* Local engagement time for each species, measured as the mean length of time an individual tried to move the cricket in a particular direction

before giving up or changing directions (species significantly differ: $F = 22.25$, $p < 0.0001$). This panel excludes one data point off the scale—one *P. longicornis* worker's local engagement time was >90 s. Horizontal line indicates the median; boxes include 50% of the data; and whiskers extend to the lowest and highest values that are within 150% of the interquartile range. Small dots are points outside that range

Table 2 Total engagement effort and local engagement time for each species. Sample sizes for these persistence measurements are included in Table 1

	Mean total engagement effort, proportion of time pulling (s.e.)	Mean local engagement time, seconds (s.e.)
<i>P. longicornis</i>	0.360 (0.0050)	8.63 (0.29)
<i>F. podzolica</i>	0.136 (0.0018)	3.62 (0.068)
<i>F. obscuripes</i>	0.093 (0.0017)	4.61 (0.072)
<i>F. pallidefulva</i>	0.0567 (0.0014)	2.35 (0.074)

pallidefulva workers rarely succeeded at moving baits (26.7% of attempts), and when they did succeed, they had the highest sinuosity, on average moving more than four times the distance necessary, indicating that these groups changed direction frequently. There were significant differences among species in the proportion of transport attempts that were successful ($\chi^2 = 10.02$, $df = 3$, $p = 0.018$). Sinuosity also differed significantly among species (Kruskal–Wallis $\chi^2 = 26.86$, $df = 3$, $p < 0.0001$). The results of Dunn post hoc comparisons of sinuosity, with Bonferroni adjustments, are shown in Fig. 4 and Table S1. *P. longicornis* had significantly lower sinuosity than all

other species, and *F. obscuripes* groups had marginally lower sinuosity than groups of *F. pallidefulva* ($p = 0.059$).

I used Kendall's rank correlation tests to determine if I could detect significant correlations between persistence and efficiency among species. Among these species, I did not find significant correlations. However, the correlation between total engagement effort and success fraction was marginal, species with higher total engagement effort tended to be more likely to succeed (Kendall's $\tau = 1$, $p = 0.0833$). My statistical approach is conservative, and this p value is the lowest possible for a two-tailed Kendall's rank correlation with four points. Likewise, the correlation

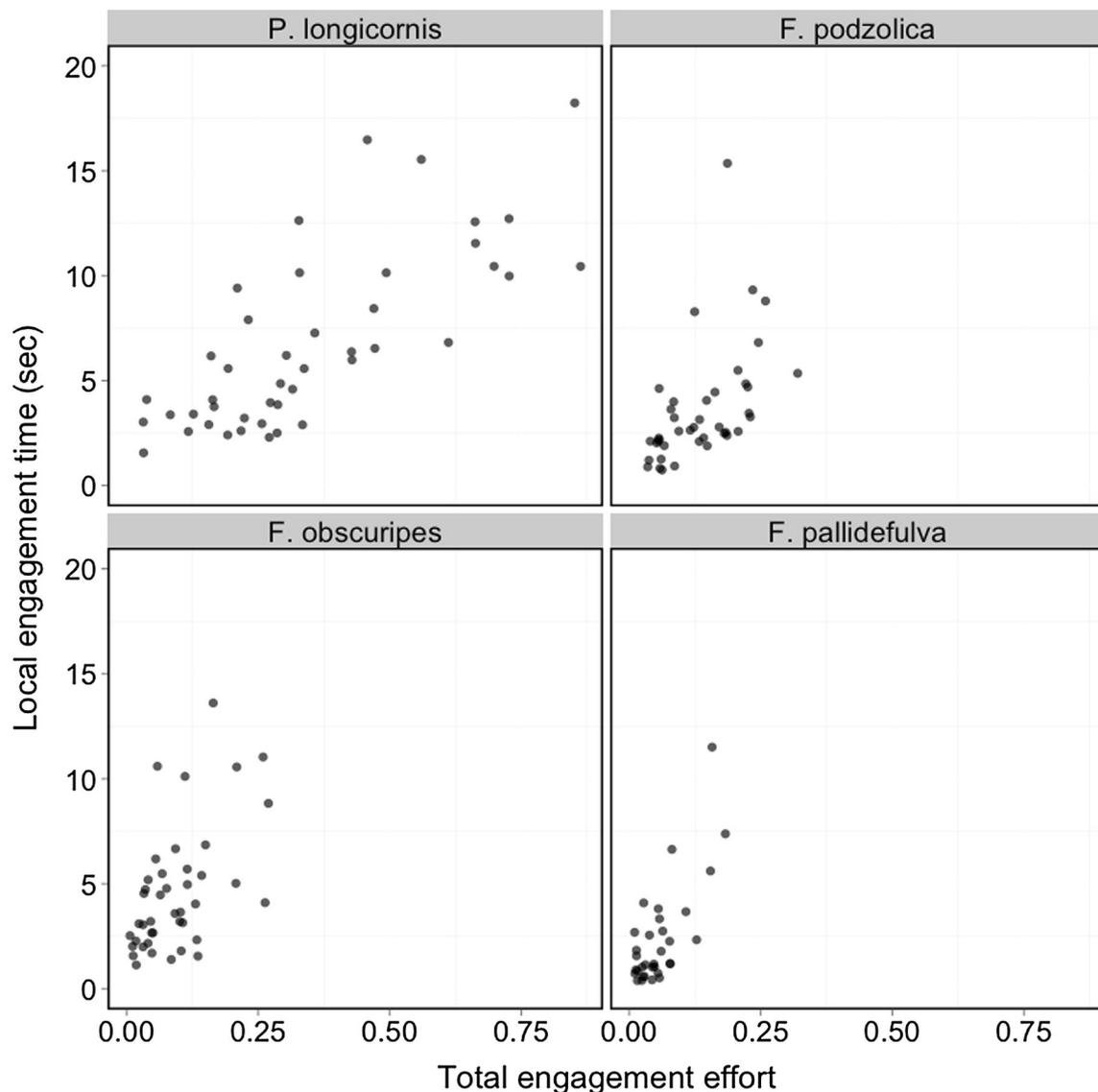


Fig. 3 Local engagement time (mean time moving a particular direction before changing) and total engagement effort (proportion of time trying to move object) are correlated in individuals in pooled data (Pearson's $r = 0.69$, $p < 0.0001$) and within each species (*P.*

longicornis: $r = 0.68$, $p < 0.0001$; *F. podzolica*: $r = 0.65$, $p < 0.0001$; *F. obscuripes*: $r = 0.54$, $p = 0.0002$; *F. pallidefulva*: $r = 0.56$, $p = 0.0007$). Figure excludes one data point off the scale—one *P. longicornis* worker's local engagement time was >90 s

Table 3 Success fraction and sinuosity in each species

	Attempts	Successes	Success fraction (%)	Mean sinuosity (s.e.)
<i>P. longicornis</i>	39	38	97.4	1.24 (0.017)
<i>F. podzolica</i>	47	45	95.7	2.14 (0.057)
<i>F. obscuripes</i>	25	22	88.0	1.94 (0.073)
<i>F. pallidefulva</i>	30	8	26.7	4.33 (0.24)

between local engagement time and sinuosity was marginal, species with higher local engagement time tended to have lower sinuosities (Kendall's $\tau = -1$, $p = 0.0833$). The

converse comparisons were not indicative of correlative relationships in the four species (local engagement time with success: Kendall's $\tau = -0.67$, $p = 0.33$; total

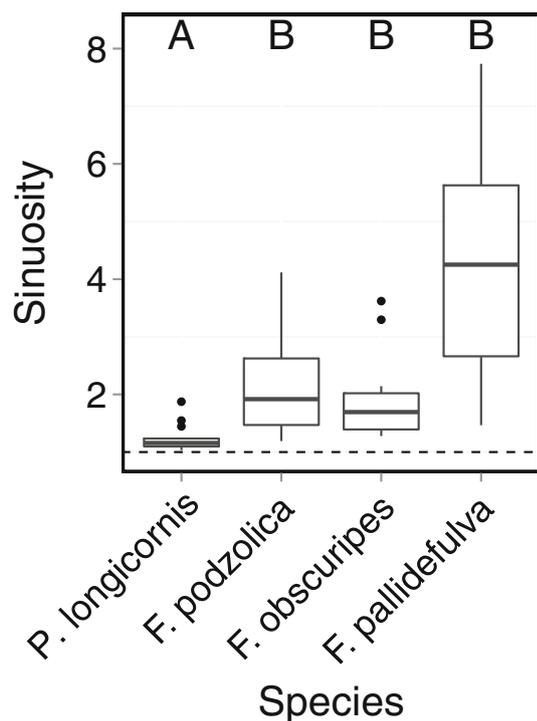


Fig. 4 Sinuosity of cooperative transport efforts for each species. Low sinuosity indicates high coordination. *Dashed line* indicates lowest possible sinuosity. Species significantly differ in sinuosity (Kruskal–Wallis $\chi^2 = 26.86$, $df = 3$, $p < 0.0001$). *Letters* indicate pair-wise significant differences, from Dunn post hoc comparisons. Sinuosity of *F. obscuripes* and *F. pallidefulva* groups moderately differed ($p = 0.059$). *Horizontal line* indicates the median; *boxes* include 50% of the data; and *whiskers* extend to the lowest and highest values that are within 150% of the interquartile range. *Small dots* are points outside that range

engagement effort with sinuosity: Kendall's $\tau = 0.67$, $p = 0.33$). While the number of species in this study limits the statistical power, the results for efficiency fit the expected pattern based on the hypotheses and persistence measurements. Species with higher individual persistence had cooperative transport groups that were more coordinated.

Does changing the behavioral makeup of groups affect sinuosity?

On average, motivated *F. podzolica* workers pull with a maximum force of 0.0044 N (s.e. 0.00023). Accounting for colony in this calculation (by first averaging within a colony), only changed the resulting force by 2%, to 0.0043 N. Within each colony, forces ranged from 0.0032 to 0.0060 N. For Study 2, I used the mean accounting for colony (0.0043 N) to determine the force the artificial ants exerted on the bait. To mimic this force, I added a weight of 0.44 g to the apparatus shown in Fig. 1b.

Sinuosity measurements before and after the addition of artificial ants are shown in Fig. 5 (white boxes: before addition, gray boxes: after addition), an example trial is shown in Online Resource 4. Control trials, with no artificial ants added, did not result in changed sinuosity, and thus, sinuosity did not naturally change over time (Wilcoxon's $W = 471$, $p = 0.61$). The addition of one artificial ant was not sufficient to improve efficiency (Wilcoxon's $W = 533$, $p = 0.31$). When two artificial ants with infinite total engagement effort and local engagement time were added to groups, sinuosity marginally improved (Wilcoxon's $W = 103$, $p = 0.074$). While the result for two artificial ants was not significant, together with the results from the species comparison, it supports a biologically relevant relationship between total engagement effort and/or local engagement time and transport efficiency.

Discussion

Ant species differ substantially in their cooperative transport ability. This variation likely arises from ecological and evolutionary differences. For example, species in areas with

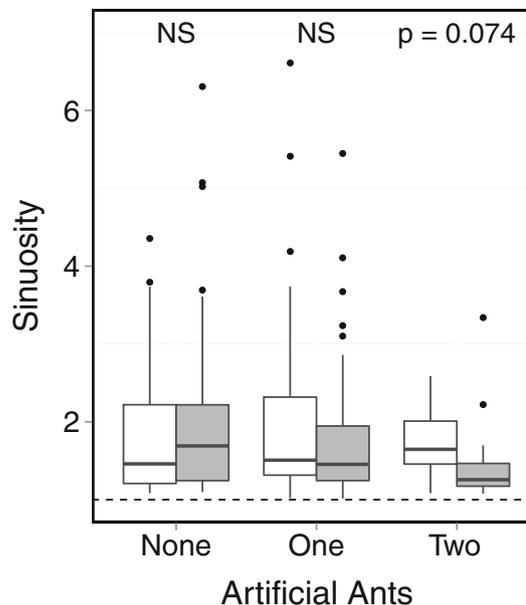


Fig. 5 Sinuosity of *F. podzolica* groups before (*open boxes*) and after (*gray boxes*) adding artificial ants. Low sinuosity indicates high coordination. *Dashed line* shows lowest possible sinuosity. Comparisons of sinuosity before and after artificial ants were added were conducted on each treatment group using paired Wilcoxon's signed rank tests. For clarity, figure excludes one point for the control group (after no artificial ants were added); in this trial, the sinuosity was 10.03. *Horizontal line* indicates the median; *boxes* include 50% of the data, and *whiskers* extend to the lowest and highest values that are within 150% of the interquartile range. *Small dots* are points outside that range

high competition for large food resources may experience higher selection pressure to engage in cooperative transport, as groups that bring food to their nest quickly less frequently lose the food to competitors (Yamamoto et al. 2008). *P. longicornis* workers may be substantially more effective at cooperative transport than *F. pallidefulva* workers, because the behavior may be more important for them. The mechanisms responsible for these differences that allow coordination to emerge in efficient groups must result in large part from traits of individuals.

As with other collective decisions, including nest-site selection in honeybees and *Temnothorax* ants (e.g., Mallon et al. 2001; Seeley 2010), I expected that individuals' enthusiasm for and fidelity to their chosen option (their persistence) might affect group coordination. I recorded the persistence of individuals at immovable baits, and I found that ant species differ substantially in both measures of persistence: total engagement effort and local engagement time (question 1). *P. longicornis* workers had a mean total engagement effort more than six times that of *F. pallidefulva*, and a mean local engagement time nearly four times as high. *P. longicornis* workers were also by far the most coordinated of these four species. Since the patterns across the four species of the two types of persistence were similar, I could not isolate the potential effects of these traits individually when evaluating questions 2 and 3. The fact that I examined only four species also limits the statistical power. However, the pattern of efficiency I observed closely matches the predictions based on theory (McCreery et al. 2016a): more persistent species were more coordinated, indicated by success in more of their attempts and lower sinuosity. One also expects groups with high variation in persistence to be more efficient, because if a small number of individuals are highly persistent with others having low persistence, the group may rapidly converge on the direction favored by the persistent ants. This hypothesis has been supported in the context of navigation during cooperative transport (Gelblum et al. 2015). My observations provide additional support for this hypothesis, as *P. longicornis* workers also had, qualitatively, the highest variation in both total engagement effort and local engagement time. Not only were *P. longicornis* groups the most efficient, but they also had low variation in sinuosity—these ants were nearly always successful, and had extremely low sinuosity in virtually all cases.

While the two types of persistence, total engagement effort and local engagement time, were correlated—species with high total engagement effort also had high local engagement time—the patterns were reversed for *F. obscuripes* and *F. podzolica*. Compared with *F. podzolica*, *F. obscuripes* individuals spent less time trying to move an object (lower total engagement effort), but were unlikely to change the direction they tried to move it (moderately higher local engagement time) (Fig. 2). The differences

were not large enough for me to disentangle the effects of these traits with confidence, but the success fraction and sinuosity results for these species suggest new hypotheses about the effects of high total engagement effort and high local engagement time separately. High total engagement effort may be more important for getting moving at all, while high local engagement time may be more important for low sinuosity. With only four species, I do not have strong evidence for these observational patterns, but these hypotheses could be explicitly tested with additional observational or manipulative experiments.

The two measures of persistence were correlated with the measures of coordination among the four species I observed. If high persistence and variation in persistence in fact promote coordination—if this correlation is causal—one expects sinuosity to improve after increasing the mean and variance of persistence in a given group (question 3). Indeed, adding two artificial, infinitely persistent ants to transport groups moderately improved sinuosity. This effect was not significant at the $\alpha = 0.05$ level ($p = 0.074$); nevertheless, my results suggest an important behavioral pattern. A string is a relatively crude ant mimic, and only reproduces a single ant cue, the physical pull that other workers may feel on the object. Yet, even with this single cue, groups to which I added two infinitely persistent ants improved enough that their median sinuosity approached the minimum possible of 1. More sophisticated mimics of persistent ants that include additional information, such as visual or pheromonal cues, should have stronger effects. I conducted this experiment in a species that does not naturally have very high persistence; perhaps *F. podzolica* workers are not strongly tuned into persistence, while other species may be. I chose *F. podzolica* for Study 2, because I needed groups that could reliably begin transport, but not so efficiently that I would not be able to see an improvement. *F. podzolica* groups fit these requirements. It would be interesting to consider similar manipulative experiments in species with high persistence and high variation, such as *P. longicornis*. Such groups may respond more strongly to persistence manipulations. It would also be valuable in the future to measure persistence and sinuosity in the same groups, such that for a group for which one had sinuosity data, one also had persistence data for each group member.

The two types of persistence which I measured were correlated; individuals with high total engagement effort tended to also have high local engagement time. As these traits also seemed to promote coordination, individuals with high total engagement effort and local engagement time may play an out-sized role in cooperative transport efforts, perhaps operating as temporary leaders. If individuals express persistence consistently through time, highly persistent individuals may be cooperative transport specialists. Alternatively, individuals may vary their persistence over

time based on the information they have. Perhaps, in coordinated species, highly persistent individuals are those with better information about the direction of the nest. It would be interesting in future studies to see if individual persistence is consistent through time, and whether it is affected by the quality of nest location information.

While my study focused on persistence, the species that I observed differ in many other traits, including traits related to cooperative transport, such as recruitment strategies, group size, and likely behavioral rules for coordination. These differences make inference difficult in among-species comparisons, and may explain why previous cooperative transport studies have not quantitatively compared species. Indeed, these challenges are present for research into other emergent group behavior as well; it is difficult to compare individual traits in groups that differ substantially in an emergent behavior of interest, in part because the individuals in such groups tend to differ in many traits simultaneously. While interpretation is difficult, the challenge of comparing groups with substantial differences does not negate the benefit of such studies. Indeed, to examine the mechanisms of emergent behavior in groups, there is a great deal of value in exploring how actual groups differ, and how traits of individuals in those groups contribute to those differences. For cooperative transport, looking across species, where one expects large group-level differences, is an important step. To my knowledge, this study is the first to do so quantitatively. My results support the hypothesis that individual-level persistence promotes group coordination, and suggest additional hypotheses about the separate effects of individual total engagement effort and local engagement time. Among the species that I observed, groups in which individuals have higher persistence are more coordinated, and increasing the mean and variance of persistence among individuals modestly increases group coordination.

Acknowledgements I thank Mike Breed for discussing conceptual design and results, and for providing comments on this manuscript. I also thank Andrew Koller for help brainstorming experimental procedures, particularly regarding measuring the force ants pull with. Zach Dix extracted persistence data from videos and assisted with the fieldwork in Arizona, and Jenna Bilek helped with additional data extraction. I thank Tomer Czaczkes and Stephen Pratt for providing valuable comments on an earlier version of the manuscript. Dr. Pratt at ASU and John Adams at Biosphere 2 provided assistance and use of their facilities during fieldwork. I thank QDT and the writing coop for providing suggestions on the analyses and/or writing. This work was funded in part by the University of Colorado Graduate School, and the Department of Ecology and Evolutionary Biology.

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