Cooperative Transport in Ants: Emergent Coordination and Collective Problem Solving

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COOPERATIVE TRANSPORT IN ANTS: EMERGENT COORDINATION AND COLLECTIVE PROBLEM SOLVING

by

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Cooperative transport in ants: emergent coordination and collective problem solving

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline
ABSTRACT

Across scales, complexity emerges within groups of simple individuals. In many cases, groups succeed at tasks that are well beyond the capabilities of individuals; this is collective intelligence. Ants provide some of the best examples of collective intelligence, and groups of ants succeed at remarkable challenges. A highly conspicuous example of such behavior in ants is cooperative transport, which occurs when a group collectively moves a large, heavy food object. Cooperative transport groups must overcome two major challenges: 1) agreeing on a travel direction and 2) navigating around obstacles. The first challenge requires breaking deadlocks to reach a consensus decision. The second requires problem solving – groups must make a series of new decisions, each building on the previous. My goal was to discover the individual- and group-level mechanisms that allow some ant species to overcome these challenges, and spectacularly succeed at cooperative transport. At the individual level, I found that theoretically, even groups of individuals with simple behavioral rules can break deadlocks. Individuals only need to determine whether they are aligned with the majority. My theoretical work also indicates that individual persistence – reluctance to change direction – promotes group consensus. I tested this hypothesis empirically, and found that species with more persistent individuals form more coordinated groups, and artificially increasing persistence increases coordination. At the group level, I discovered that object size and mass affect group coordination time and speed, but not the maintenance of coordination. Finally, in a species of expert transporters, groups excel at maintaining consensus while navigating obstacles, and they add complexity to their navigation strategy only if simpler behavior fails. My dissertation contributes to our understanding of emergent group behavior by demonstrating simple behavioral rules and a trait – persistence – that promote consensus. I have identified object properties that influence transport in surprising ways, and found that groups use a flexible and robust problem solving strategy for obstacle navigation. This work elucidates important mechanisms that allow some species to excel at cooperative transport.
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CHAPTER 1

INTRODUCTION

From molecular dynamics within cells to massive animal migrations, emergent group phenomena are ubiquitous and drive much of the complexity of the natural world (Camazine et al. 2001; Sumpter 2010). This includes organization from abiotic groups, such as sand grains forming ripples on a beach (Kok et al. 2012), up to groups in which the individuals are, themselves, complex entities, such as collective movement in schools of fish (Couzin et al. 2002). As with grains of sand forming ripples, no individual in a school of fish has global information; rather, group behavior emerges from local interactions among individuals. Such emergent phenomena often allow groups to accomplish tasks that are well beyond the capabilities of the individuals in those groups; this is known as collective, or swarm, intelligence (Dorigo et al. 2006; Garnier et al. 2007). Biological collective intelligence arises through some common mechanisms, including stigmergy – a form of indirect communication through local environment modification – and both positive and negative feedbacks (Garnier et al. 2007). Such self-organized processes allow for decentralized control of complex processes. Complex cognitive abilities, including our experience of consciousness, emerge from networks of comparatively simple neurons in the brain (Menon 2013). The mechanisms that allow groups to coordinate can be similar even across disparate systems. To continue with the example of neural networks, the decision-making process in groups of neurons in primate brains is closely analogous to the nest-site selection process in some social insects, including honey bees and Temnothorax ants (Pratt et al. 2002; Pratt 2005; Marshall et al. 2009; Seeley 2010; Seeley et al. 2012a; Pais et al. 2013), despite obvious, large differences between individual neurons and social
insect colonies. Thus, by studying emergent complexity in one group we may gain insight into other systems that are more difficult to study.

Ants are excellent model systems for research in collective intelligence for two reasons. First, ants are relatively easy to study, as one can often separately observe and manipulate individuals in a group. Second, and perhaps more importantly, ant colonies provide some of the best examples of collective intelligence. The disparity between what individual ants can accomplish and what entire colonies accomplish is remarkable. Army ants in the Eciton genus are blind, and rely entirely on pheromone trails that they lay for navigation. Yet colonies explore large areas of forest every day to find their preferred food, maintaining robust foraging trails hundreds of meters long (Schneirla 1971). They self-assemble into bridges to maintain high traffic flow in rough terrain (Reid et al. 2015b), and move the whole colony of hundreds of thousands of individuals every night, self-assembling into elaborate structures to form temporary nests (Schneirla 1971; Hölldobler and Wilson 1990). Most ant species construct more permanent nests, which are often large, with chambers dedicated to specific purposes—Atta cephalotes leaf-cutter ants, for example, construct specialized chambers within their massive, underground nests in which to grow fungal gardens for consumption (Hölldobler and Wilson 1990). Collective intelligence in ants is not limited to nest construction. The vast majority of necessary tasks in ant colonies are accomplished with decentralized control, including larval care, foraging, hygienic behaviors, and more. Ants are a model system for collective intelligence, and ants have also provided inspiration for decentralized control research in computer science and engineered systems (Kube and Bonabeau 2000; Dorigo et al. 2006).

A particularly conspicuous example of collective intelligence in ants is *cooperative transport*, or the movement of a large, heavy food item, intact, by a group working together
Cooperative transport allows some ant groups to carry objects many thousands of times the mass of each individual (Wojtusiak et al. 1995), and for some species it is an ecologically important strategy for food collection – in *Pheidole oxyops* colonies, for instance, 78% of the food mass consumed by colonies was brought to the nest via cooperative transport (Czaczkes et al. 2011). While some species are able to carry dead vertebrates, including birds, bats, and snakes, vertically up tree trunks to their nests (Wojtusiak et al. 1995), most ant species do not coordinate their transport efforts, and rarely succeed at cooperative transport (Moffett 1992; Czaczkes and Ratnieks 2013). Outside of ants and humans, cooperative transport rarely occurs in nature, suggesting that cooperative transport is a difficult challenge. Indeed, cooperative transport poses a sufficient challenge that it is a common task in studies of robotics, and a substantial body of literature focuses on the design of robot groups that can carry objects together (e.g. Kube and Bonabeau 2000; Berman et al. 2011; Rubenstein et al. 2013; Wilson et al. 2014). We have not succeeded at building groups of robots that can accomplish what some ant species do: collectively carry a heavy, arbitrarily shaped object to a specific goal over highly heterogeneous terrain.

Cooperative transport requires groups of animals to overcome several sub-tasks, or phases, in the transport process. These steps are outlined in Chapter 2. My research has focused on two major challenges of cooperative transport that many species fail to overcome. First, once a sufficient number of individuals has assembled near an object, the group must make a collective decision about travel direction. In many ant species, groups fail to make this decision, and transport attempts are characterized by long deadlocks, as individuals pull in opposing directions (Moffett 2010; Czaczkes and Ratnieks 2013). Groups that are successful at forming a consensus about travel direction must overcome the second challenge I have focused on, which
is navigating around obstacles to move over heterogeneous terrain as they travel to their nest. Obstacles present particularly difficult problems for groups of ants for two reasons: 1) groups must make a new decision on a direction to move around the obstacle when their preferred direction – toward the nest – is blocked, and 2) groups must continually update this decision, in fact making a series of decisions, each building on the previous. Obstacle navigation requires transport groups to solve problems.

The overall goal of my dissertation was to explore the individual- and group-level mechanisms that allow some species to succeed cooperative transport. In Chapter 2, I review existing literature on proximate mechanisms of cooperative transport. I discuss each phase of cooperative transport, and present hypotheses about individual mechanisms that may promote coordination. In Chapter 3, I present an empirical study on the effects of object properties – mass and size – on group behavior and cooperative transport success during the beginning of transport – i.e. the collective decision about travel direction and the immediate results of that decision. This was a knowledge gap, as previous studies had not isolated the effects of size and mass, and previous mechanistic studies had not evaluated how object properties affect transport.

Chapter 4 presents a theoretical study of individual-level traits that affect the collective decision about travel direction, and especially deadlock-breaking. I evaluated the consequences of different types of behavioral rules, as well as other individual traits including persistence and sensitivity, and discovered that individual complexity is not required. In a theoretical context, even groups of simple individuals, with minimal information available, can break deadlocks to form consensus. This work also led to a new hypothesis, that individual persistence promotes group coordination. I tested this hypothesis empirically, with experiments presented in Chapter 5. I compared individual persistence and group cooperative transport success across four species,
finding that more coordinated species had individuals with higher persistence. I also manipulated groups in one species, finding that increasing persistence increased coordination.

As discussed in Chapters 3 and 5, *Paratrechina longicornis* ants, or long-horn crazy ants, are remarkably coordinated about travel direction, and do not seem to deadlock. Thus, I chose this species as a study system to evaluate how groups navigate around obstacles. In work presented in Chapter 6, I identified elements of *P. longicornis* workers’ obstacle navigation strategy, examining both the individual- and group-levels. I demonstrated that groups of *P. longicornis* workers are remarkably effective at maintaining consensus while they implement a flexible and robust problem solving strategy. I found that in some cases, I could identify direct individual contributions to that strategy, but many important decisions seemed to emerge from the group with no clear individual impulse. The strategy of *P. longicornis* groups allows them to rapidly navigate around simple obstacles, while succeeding at difficult obstacles that require moving away from their goal, the nest. Finally, in Chapter 7 I synthesize the overall results and implications of my dissertation.
CHAPTER 2

Cooperative transport in ants: a review of proximate mechanisms

2.1 ABSTRACT

The behavioral mechanisms that lead to cooperation in social insects are often unknown or poorly understood. Cooperative transport, or the movement of an object by two or more individuals, is a particularly impressive example of collaboration among workers. Many ant species perform this behavior, but there is extreme interspecific variation in efficiency. Why are some ant species so efficient at cooperative transport, while others are so inefficient? Surprisingly, the scientific community has little proximate understanding of the adaptations that make certain species excel at this behavior. This work provides a review of the behavioral rules that separate the efficient cooperative transporters from the inefficient. We present two measures of efficiency of cooperative transport as well as a flowchart of the cooperative transport process. By identifying the steps and flow of information, the flowchart enables careful modeling of cooperative transport from a mechanistic perspective. Previous studies of each of the four phases of cooperative transport are discussed, including decision, recruitment, organization, and transport. We also present hypotheses regarding behavioral mechanisms that may modulate efficiency.

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1This paper was published in *Insectes Sociaux* with Michael D. Breed
2.2 INTRODUCTION

Social insects show remarkable cooperation in diverse tasks, yet the proximate mechanisms that lead to collaboration among workers are often poorly understood. Cooperative transport, which occurs when a group of individuals work together to move an otherwise unmanageable object, is the subject of this review. Cooperative transport is known in at least 40 genera of ants (Hölldobler and Wilson 1990; Moffett 1992; Czaczkes and Ratnieks 2013), though not all of these genera exhibit efficient transport. Efficient cooperative transport requires a high degree of coordination among workers. The mechanisms that support this coordination are largely unknown. One might expect foraging workers to attempt to retrieve any appropriate piece of food they find, whether a prey item, a carcass, or a seed. Yet some food items, such as large arthropods, are too large or heavy for a single worker to carry. Thus cooperative transport of food is a proximate behavioral mechanism that increases the size range of food available to a colony. Here, we review behavioral mechanisms that lead to cooperative transport. We also present new conceptual models of behavioral parameters that lead to remarkable efficiency in transport efforts.

Considering its ecological importance and applications, cooperative transport is understudied. Ant species that have evolved this capability increase the amount of food accessible to them (reviews: Berman et al. 2011; Czaczkes and Ratnieks 2013). For some species, food transported cooperatively makes up a large proportion of total food mass collected by the colony: e.g. 78% of food mass for *Pheidole oxyops*, (Czaczkes et al. 2011); 64% of prey mass for *Dorylus wilverthi*, (Franks et al. 1999). In some habitats, the quality of food available by cooperative transport may be higher than that available by individual transport. Although this has not been explicitly documented, in habitats where small protein sources are rare, an insect
carcass too large to be transported individually is a vital source of protein for a colony. Quickly transporting a large food item back to the nest, instead of dissecting it in place, also reduces the amount of time the food is vulnerable to competition (Hölldobler et al. 1978; Yamamoto et al. 2008). Cooperative transport therefore represents an important aspect of the ecology of many ant species.

Successful transport generally requires a mechanism to attract more than one worker to the food and the formation of a consensus about direction of travel. Ant species exhibit extreme variation in cooperative transport efficiency. For example, *Oecophylla longinoda* workers collectively carry birds, bats, and snakes vertically up a tree trunk (Wojtusiak et al. 1995), whereas in other species worker groups pull food items in opposing directions for minutes or hours, making little or no progress. This variation suggests that attraction and/or consensus mechanisms are absent in inefficient ant species, and that cooperative transport evolves in response to specific trophic challenges (Yamamoto et al. 2008). In species that are poor at cooperative transport, the arrival of workers at the food appears to be haphazard and the movement of the food item is inefficient as groups are unable to coordinate the direction of travel (Moffett 2010; Berman et al. 2011; Czaczkes and Ratnieks 2013). In species that are efficient at cooperative transport, additional workers arrive at the food quickly, and transport progresses rapidly in a straight line toward the nest (Berman et al. 2011; Czaczkes and Ratnieks 2013). This variation in degree of coordination makes cooperative transport an interesting and informative task for the study of animal cooperation in general.

What allows for impressive coordination of cooperative transport in some species, while most species are inefficient? Efficient species may have evolved specific behavioral rules that facilitate group coordination. In a recent review of cooperative transport, Czaczkes and Ratnieks
(2013) outlined some adaptations for cooperative transport. For example, in *Formica incerta* – referred to as *Formica schaufussi* in the original publication (Trager et al. 2007) – the coordination of the transport effort depends on the presence of the worker that originally found the food, the “scout” (Robson and Traniello 2002). If the scout is removed, the transport effort fails (Robson and Traniello 2002; Czaczkes and Ratnieks 2013). Moffett (1992) and Berman, et al. (2011) also reviewed cooperative transport in ants and provided helpful insight. However, still missing from the literature is a complete picture of the behavioral rules present in some ant species that allow them to excel at this behavior, separating them from inefficient transporters.

We examine proximate mechanisms of cooperative transport, adding to concepts presented in the previous reviews.

Here, we: 1) define cooperative transport; 2) generate a model of the stages of cooperative transport and summarize previous research on mechanisms for each stage; 3) define measures of transport efficiency; 4) discuss species-level parameters that may modulate transport efficiency; and 5) discuss challenges in researching behavioral rules and ways of overcoming these challenges. In each of these sections we build on previously published research on cooperative transport to provide new insights.

2.3 WHAT IS COOPERATIVE TRANSPORT?

We define cooperative transport as two or more workers grasping an item and moving it intact to another location. Cooperative transport does not include behavior where workers separately move pieces of a dissected object; this separates cooperative transport from other types of cooperative foraging. One may argue that not all incidents of cooperative transport are actually cooperative. Transport could emerge from workers following the same behavioral rules
as they do while individually foraging. For the purpose of this paper, and to be consistent with transport as defined by Czaczkes and Ratnieks (2013), we include even this uncoordinated transport in our definition of cooperative transport. Cooperative transport is also referred to as group retrieval (e.g. Berman et al. 2011).

Species that engage in cooperative transport can be subdivided into categories based on characteristics of the transport. Czaczkes and Ratnieks (2013) defined three such categories, or syndromes (sensu Czaczkes and Ratnieks 2013). The first is uncoordinated cooperative transport, which results in slow progress as workers simultaneously push or pull the object in multiple directions. Czaczkes and Ratnieks (2013) note that uncoordinated efforts are punctuated by frequent “deadlocks,” in which two or more workers pull in opposing directions, each attempting to drag the item backwards from her current position (Czaczkes and Ratnieks 2013). Encircling coordinated transport, the second category, is characterized by fairly rapid transport with few, short-lived deadlocks. Workers at the leading edge of the food pull, while workers at the back either push or reduce drag by lifting the food (Czaczkes and Ratnieks 2013). The third category, forward-facing coordinated transport, is characterized by rapid transport without deadlocks, in which all workers face the direction of travel (Czaczkes and Ratnieks 2013). Army ants typically fall into this category (Franks 1986; Franks et al. 2001; Czaczkes and Ratnieks 2013).

Placing ant species into these categories advances the field of cooperative transport research by providing context for the evolutionary history of the behavior. Cooperative transport occurs in a range of genera across several subfamilies of ants (Hölldobler and Wilson 1990; Moffett 1992; Berman et al. 2011; Czaczkes and Ratnieks 2013), suggesting that multiple evolutionary origins of this behavior are likely. However, no explicit phylogenetic analysis of the behavior has been conducted. Categorizing ant species as proposed by Czaczkes and Ratnieks (2013) will simplify
such an analysis and improve our understanding of the evolution of this behavior. Before we can complete such an analysis, however, more comprehensive data are required to categorize species.

2.4 PHASES OF TRANSPORT

Figure 2.1 shows the steps and feedbacks of a typical cooperative transport effort with a flowchart. Within this general framework, the precise processes, mechanisms, and outcomes vary greatly among species. In ant species that are efficient at cooperative transport, the effort may proceed as follows:

1. A forager finds a piece of food too large for her to transport alone. In species with active recruitment, the forager must decide to recruit additional workers (decision phase, see Figure 2.1).

2. The forager recruits other workers to help with the transport (recruitment phase).
   Recruitment strategies differ, but often involve returning to the nest and leading additional workers back to the food. Recruitment is not necessary if additional workers are attracted to the food or accumulate by chance.

3. In some species, certain workers in the group establish or maintain specific roles, and/or form a consensus on the direction of travel (organization phase).

4. Together, the accumulated workers move the item – without dissection – toward the nest (transport phase).
Figure 2.1: Generalized process of cooperative transport. Corresponding phases as described in text shown on the right. The distinction between the two paths of the flowchart corresponding to “Information transfer” and “No information transfer” is likely a gradient.
These four phases of a cooperative transport effort are described in further detail below. The degree to which these phases have been studied varies, and none have been studied to an extent that overarching lessons can be learned about cooperative transport in all ants. Also missing from the literature is evidence for the particular proximate mechanisms that govern most aspects of the behavior. Therefore, we summarize the research on each of the phases with examples from particular species, and identify gaps in which additional research would be fruitful.

**Decision Phase**

In some species the decision to engage in cooperative transport is adaptive, and is based on the likelihood that the transport would succeed. An ant colony that attempts cooperative transport for every large piece of food they find wastes effort on transports that cannot succeed. Decisions about whether to attempt transport therefore increase fitness, if they are fairly accurate. This section summarizes the results and implications of previous research into cooperative transport decisions.

Sometimes a decision is not necessary. Cooperative transport could emerge as workers accumulate at a food item. However, in ants that actively recruit helpers, the worker that finds the food must decide to initiate cooperative transport. This decision modifies her recruitment efforts. Several ant species adjust the number of workers they recruit based on the size and type of prey (Detrain and Deneubourg 1997; Cogni and Oliveira 2004; Cerda et al. 2009). For *Pheidole pallidula*, a load’s resistance to movement affects the decision to engage in cooperative transport (Detrain and Deneubourg 1997). *P. pallidula* recruits differently to a pile of fruit flies (individually transportable) than to a cockroach (Detrain and Deneubourg 1997). The recruitment
to the cockroach is much faster, with many workers arriving at the food quickly, while the recruitment to fruit flies is gradual (Detrain and Deneubourg 1997). This indicates that there is more than one mode of recruitment, and that workers use characteristics of the food item to decide which type to elicit. When presented with a pile of immovable fruit flies (pinned under a net), recruitment was closer to that associated with a cockroach, suggesting that the resistance of the load is a parameter that affects the decision (Detrain and Deneubourg 1997).

In the neotropical ant Gnamptogenys sulcata, prey size and mass are parameters that interact to affect recruitment decisions (Daly-Schweitzer et al. 2007). In this ant species, unusually, the foraging is conducted by a very small number of highly specialized hunters; there are only 1–4 hunters in each colony (Daly-Schweitzer et al. 2007). Once the prey is immobilized, these hunters can recruit other workers (non-hunters) to help with the transport. Daly-Schweizer et al. (2007) observed recruitment behavior for various prey types. Prey that were less than 8.5 times the mass of the hunter never prompted recruitment, while prey with a mass more than 21 times the hunter’s always prompted recruitment (Daly-Schweitzer et al. 2007). For intermediate prey masses, the recruitment response varied, with both prey size (independent of mass) and type of prey affecting the decision (Daly-Schweitzer et al. 2007).

In Cataglyphis floricola, workers do not initiate recruitment if the probability of recruits finding the food is low. This genus lives in arid environments where volatile compounds very quickly evaporate (Amor et al. 2009), so they are not able to use trail pheromones to direct other workers. Members of C. floricola that find a large food item can recruit helpers from the nest, but are not able to provide any information about location of the food; recruited workers simply search in the vicinity of the nest (Amor et al. 2009). If a recruit locates the food, she stays there until enough workers accumulate to carry the food to the nest (Amor et al. 2009). This
recruitment is only successful over short distances. Workers that find food items more than one meter from the nest entrance do not even attempt recruitment (Amor et al. 2009). This indicates that recruitment, and cooperative transport, is an active decision determined by proximity to the nest. Workers must be capable of keeping track of distance, at least approximately, and using this distance to inform their decision. In another *Cataglyphis* species, *C. niger*, recruitment behavior is governed by simple behavioral algorithms regarding interactions in the nest (Razin et al. 2013).

We have outlined a few cases where there is evidence for particular decision parameters, including load resistance, load size and mass, type of food, and probability that the food will be found by recruits. However, for most ant species the parameters affecting the decision are unknown. Research on decision parameters in additional species would allow for cross-species comparisons and a synthesis of decision-making in cooperative transport.

*Attraction/Recruitment Phase*

Attraction and recruitment mechanisms vary greatly among species, and synthesizing lessons about recruitment in general is difficult. Here, we summarize the results of previous research focusing on active recruitment for cooperative transport, and briefly discuss passive recruitment. Recruitment has been studied more extensively than the other phases of transport, so here we present examples from a broader literature.

In species that actively recruit helpers, this recruitment phase generally involves two steps. The worker that found the food (the “finder”) returns to the nest or a central location and notifies nest-mates of the food using pheromones or another signal. In some species the finder also leads the recruited workers directly to the prey item (Amor et al. 2009). For example, in *G. sulcata*, the finder recruits by laying a chemical trail on her way back to the nest (Daly-
Schveitzer et al. 2007). After alerting nest-mates, she re-marks the chemical trail back to the prey item. The recruited nest-mates follow her, though not immediately (Daly-Schweitzer et al. 2007). Similar recruitment behavior is observed in *Formica incerta* (Robson and Traniello 1998), *Aphaenogaster cockerelli* – formerly *Novomessor cockerelli*, (Hölldobler et al. 1978), and others.

In *G. sulcata*, recruitment is always initiated by the hunter that found the prey. This hunter starts serial waves of recruitment if transport continues to fail (Daly-Schweitzer et al. 2007). Daly-Schweitzer et al. (2007) investigated this using an approach developed by Breed et al. (1987). They pinned a prey item to a sponge, so that no matter how many recruits attempted to transport the prey, they were unlikely to succeed. This resulted in a massive recruitment effort by the hunter, with several waves of recruitment. Eventually, the prey was torn from the pin. Each recruitment wave was initiated by the hunter that found the prey; recruits never recruited more workers (Daly-Schweitzer et al. 2007).

The pheromone trail or parameters associated with recruitment for cooperative transport can be adapted to the task (Detrain and Deneubourg 1997; Czaczkes et al. 2013). Unlike recruitment to food sources that can be individually carried, recruitment for cooperative transport is an all-or-nothing event. The colony either successfully transports the entire item, or gets nothing. Large food items are also susceptible to competition. Therefore, eliciting rapid, strong recruitment to an item requiring cooperative transport is adaptive, as exhibited by *P. pallidula*, discussed in the Decision section above (Detrain and Deneubourg 1997). Once a cooperative transport effort is complete, additional workers should no longer follow a recruitment trail, as the food is gone. Thus pheromone trails adapted to cooperative transport recruitment should be short-lived. *Pheidole oxyops* and *Paratrechina longicornis* lay recruitment trails associated with cooperative transport that are adapted for the task. In both of these species the trails decay

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quickly (in 5-7 minutes) and can be followed with high accuracy (Czaczkes et al. 2011, 2013). These short-lived trails only last long enough for a worker recruited from the nest to reach a food item within four meters (Czaczkes and Ratnieks 2013). Both species are also capable of recruiting workers who are already foraging, increasing the distance from the nest over which recruits can find food (Czaczkes et al. 2011, 2013). Local recruitment is discussed further below. Trail pheromones in *P. oxyops* and *P. longicornis* are adapted to the cooperative transport task, in which rapid, accurate recruitment is necessary to quickly move the food and avoid competition.

Not all ant species recruit to large food items by laying a pheromone trail and returning to the nest. In *Onychomyrmex hedleyi*, an army ant, the finder does not return to a central location. Instead, she antennates nearby workers. Some of these workers immediately join the finder at the prey and try to move it, while others recruit more workers from the nest (Miyata et al. 2009). This more immediate recruitment is practical in army ants with group foraging, in which there are likely to be colony members close to any forager. As discussed above, *C. floricola* has lost the ability to recruit using trail pheromones (Amor et al. 2009). Yet this species still recruits to food, provided the food is close enough that additional workers can find it with a simple search (Amor et al. 2009).

Active recruitment described above is not necessary for the accumulation of workers at a food item. Instead, additional workers may find the food separately, either by chance or because they are attracted to it. In the group-predatory ant *Proatta butteli*, workers capturing large prey rely on chance for the accumulation of helpers, at least initially (Moffett 1986). Because this species has high foraging densities, additional workers arrive quickly even without recruitment.
Assuming recruitment is occurring when workers assemble at food is not always valid.

Organization Phase

Organization is an important phase that differentiates efficient from inefficient transporters. Yet in most ant species very little, if anything, is known about how and to what extent organization takes place. In some species workers do not seem to organize themselves for the transport effort at all. Indeed, with some species that are inefficient cooperative transporters, groups pull in different directions for minutes or hours before an overall motion in the direction of the nest is achieved (Moffett 1992; Berman et al. 2011). In these ants organization is haphazard at best. However, there are ant species that are impressively efficient at cooperative transport, with a relatively short period in which workers pull in several directions (Berman et al. 2011; Czaczkes and Ratnieks 2013). In this section we discuss the results and implications of studies of organization in cooperative transport.

Groups optimize efficiency of transport if they are organized with respect to direction of travel and size of the group. Effort is wasted if there are more workers in a transport group than are needed to move the object, though extra workers may defend prey (Traniello and Beshers 1991). Several species, including *F. incerta* (Robson and Traniello 1998), *Eciton burchellii* and *D. wilverthi* (Franks et al. 2001), do match the size of the group to the size the food. This can occur without workers assessing the size of the food (Berman et al. 2011). In *F. incerta* (*F. schaufussi*, see parenthetical note above), the prey mass is significantly correlated with the size of the transport group, but not with the number of recruits that leave the nest; thus, the size-matching process occurs just prior to or during transport, rather than at the recruitment phase (Robson and Traniello 1998). In *Eciton burchellii* and *D. wilverthi*, if effective size-matching
does not occur before the transport starts, a large worker leaves a transport group when she is not needed (Franks et al. 2001); this simple rule is a proximate mechanism that leads to transport groups of an appropriate size. *E. burchellii* has a submajor caste that specializes in transport.

Franks (1986) found that in this species, transport groups tend to include a single submajor, with minor workers making up the remainder of the group. Transport groups with either zero or more than one submajor were less common (Franks 1986). Since most prey can be cooperatively carried with just one submajor, this suggests that effective size-matching occurs in *E. burchellii*.

In *Formica incerta* when a worker recruits other workers to help carry a food item, distinct roles are established for the duration of the effort (Robson and Traniello 2002). The worker that originally found the prey (the "scout", *sensu*, Robson and Traniello 2002) is more important to the success of the transport than the recruits (Robson and Traniello 2002). Robson and Traniello (2002) experimentally removed the scout after she recruited workers, on the trip back to the prey. The scout’s removal led to a failure of the retrieval effort in every case (Robson and Traniello 2002). Moreover, this was not necessarily because the recruits failed to find the prey – in about half the attempts they successfully located the prey but still abandoned the retrieval effort (Robson and Traniello 2002). The scout and recruit roles were plastic; a scout in one transport effort might be a recruit in the next. The only factor deciding whether a particular worker is a scout is whether she originally found the prey (Robson and Traniello 2002). If a single recruit succeeded in reaching the prey she was sometimes able to switch to the role of a scout and begin the recruitment process again, however, this rarely happened. Instead, this worker became disoriented, abandoned the prey and searched in other locations, or returned to the nest without recruiting more workers (Robson and Traniello 2002). Why can these ants easily
change roles between transport efforts but not within an effort? This should be studied further in *F. incerta* and other species.

**Transport Phase**

Efficient transport occurs in diverse species from several subfamilies. *E. burchellii* workers are able to transport items cooperatively just as quickly as workers transporting items individually; the speed does not depend on the size of the item being transported (Franks 1986). In several species “superefficient” transport groups have been documented; these groups are able to carry more mass cooperatively than the combined mass of what they could carry individually, including *E. burchellii* and *D. wilverthi*, (Franks et al. 1999); *Pheidologeton diversus*, (Moffett 1988); *A. cockerelli* (Hölldobler et al. 1978). These superefficient teams have been observed in species with both encircling and forward-facing coordinated transport.

In ant species with forward-facing transport, workers generally do not grasp the item all at once. Instead, a large worker begins moving the item and additional workers join the effort (Franks et al. 1999). Thus workers that join add to work that has already begun. Franks (1986), described a simple rule that could lead to this joining behavior: workers continue joining the effort until the speed of transport matches the overall traffic speed of the foraging column. This putative rule also naturally results in transport groups well matched in size and strength to what is needed (Franks 1986; Berman et al. 2011).

In contrast, for transport efforts in which even slow movement is impossible without a sufficient number of workers, group members must work together to initiate movement. If workers have behavioral rules adapted for cooperative transport, then they behave in ways that increase efficiency. In *Pheidole oxyops*, workers preferentially grasp the object at corners, which increases speed of transport (Czaczkes et al. 2011). Workers also preferentially carry from the
front and back of an object, as opposed to the middle (Czaczkes et al. 2011). Daly-Schweitzer et al. (2007) found that G. sulcata workers sometimes take turns carrying heavy prey. If there are more recruited workers than can grasp the prey at one time, the extra workers remain near the prey as it is transported, joining the transport effort as transporters leave (Daly-Schweitzer et al. 2007). Thus, the effort of transporting an object is rotated through the available workers even though they cannot all participate at one time.

Adaptive mechanisms can also emerge during a transport without requiring specific behaviors or rules. Czaczkes and Ratnieks (2011) found that P. oxyops reorient food items to reduce drag (P. oxyops do not lift food items entirely off of the ground). Items were turned significantly more frequently when the reorientation would decrease, as opposed to increase, drag (Czaczkes and Ratnieks 2011). During the turning process, a small number of workers in the group (usually one) were crucial to the turning process. These were typically workers at a corner far from the turning point – those with the most leverage. Removing this “steering ant” typically stopped the reorientation (Czaczkes and Ratnieks 2011). There was apparently nothing distinctive about the steering ant other than its placement on the food item. An object may naturally turn to an orientation that reduces drag as it gets caught on a substrate; this adaptive turning behavior likely emerges from the drag and load characteristics, rather than specialized turning behaviors (Czaczkes and Ratnieks 2011).

In F. incerta, the average “prey delivery rates” (rate of food mass collected per worker) for cooperative and individual transport do not differ (Traniello and Beshers 1991). However, as expected, individual transport is more efficient (higher delivery rate) for small prey, while cooperative transport is more efficient for large prey (Traniello and Beshers 1991). Not all F. incerta workers that help transport large prey contribute efficiency in terms of delivery rate.
When workers were experimentally removed from transport groups, the transport speed did not change, but smaller groups were less able to defend the prey against competing ant colonies (Traniello and Beshers 1991). The group members in a cooperative transport effort can have multiple functions.

Berman et al. (2011) measured the forces imparted by *A. cockerelli* workers on the object during the transport phase of cooperative transport. They documented an initial period of low coordination followed by higher coordination and velocity; the transition between these periods was characterized by a reduction in the extent to which workers were pulling in opposing directions (Berman et al. 2011). Sudd (1960) estimated forces exerted by groups of *Pheidole crassinoda* using prey attached to calibrated glass fibers. He estimated the friction between the prey and the ground and calculated forces by measuring the extent to which the fibers were bent (Sudd 1960). The total force exerted by the workers was highest when all workers in the group were pulling in the same direction (Sudd 1960), as expected.

### 2.5 MEASURES OF EFFICIENCY

We propose quantitative efficiency measures with the goal of improving the precision of comparisons of transport across species. There are two broad ways to consider efficiency of a transport effort. One is from the perspective of nest provisioning; transport efforts are efficient if they move food quickly to the nest. From this perspective, transport groups must be accurate with respect to nest direction. One can also consider efficiency from the perspective of movement with little wasted effort, without regard for nest provisioning; from this perspective efficient transport groups need not move in the direction of the nest. Of course, it is not adaptive for a transport group to move an object away from the nest, even if the movement is very fast.
However, an ‘efficient’ group that moves in the wrong direction must still be coordinated. For studying proximate mechanisms both types of efficiency are useful. We therefore propose two measures of efficiency of cooperative transport: one measures efficiency of nest provisioning, the other measures coordination without regard for accuracy of direction.

The first efficiency measure is based on the overall rate of food delivery to the nest. For a particular transport effort, we define the rate of delivery, $R$, as a flow rate per worker (grams–meters per second per worker):

$$R = \frac{mV}{N}$$

where $m$ is the mass of the object being carried, $N$ is the number of workers in the transport group and $V$ is the component of the object’s velocity vector that is pointing toward the nest.

Researchers interested in movement efficiency without regard for accuracy of direction may find a slightly different flow rate, with object speed (path-length divided by time) in place of $V$, to be more appropriate for some questions. Moffett (1988) introduced a very similar “efficiency index,” which was simply mass multiplied by speed.

For some questions, it is important to also record food delivery rate for individual transport, as done by Traniello and Beshers (1991) for *F. incerta*, using a different measure of food-delivery rate. The ratio of the mean food delivery rates for cooperative transport and individual transport is a quantitative measure of efficiency for a colony. This efficiency ratio measures a similar aspect of efficiency as Franks *et al.* (1999). Franks *et al.* (1999) evaluated the marginal increase in object mass that a group could carry for each additional unit of transport group mass. Franks’ *et al.* measure is valuable, but does not account for transport velocity, as our measure does by incorporating $V$. For our proposed efficiency ratio to be in a range of contexts, the total mass of objects carried cooperatively and individually must be equal. For example, one
might compare the efficiency of cooperatively transporting a 1 gram cricket whole with
efficiency of individually transporting a 1 gram cricket that has been dissected into 20 pieces.

\[
Efficiency\ Ratio = \frac{mean(R_{\text{cooperative}})}{mean(R_{\text{individual}})}
\]

The efficiency ratio measures efficiency of cooperative transport, standardized by efficiency of
individual transport. Ratios among species can therefore be directly compared. If an ant species
has an efficiency ratio greater than one, the efficiency of cooperative transport is higher than that
of individual transport, suggesting that the species likely has behavioral adaptations for this
group task. In contrast, if the efficiency ratio is less than one, the rate of food delivery is reduced
when cooperative transport is attempted suggesting that such adaptations might not be present.

Even for species with an efficiency ratio less than one there are some situations that
would favor cooperative transport. If the type of food available via cooperative transport is
different from that available via individual transport – e.g. if the main source of protein is large
carcasses – then a colony benefits from engaging in cooperative transport even if it reduces the
rate of delivery of food. The efficiency ratio therefore does not correlate directly with colony
fitness. Nevertheless, this measure allows for quantitative species comparisons and identifies
species where adaptations are likely.

We also suggest sinuosity as an efficiency measure that does not consider accuracy with
respect to nest direction. The sinuosity of a transport effort is the ratio of the path-length to the
shortest possible path (path displacement, Figure 2.2). High sinuosity indicates that the group
changed direction many times, and did not take a direct path. Low sinuosity indicates that the
path taken is close to the shortest possible path, which suggests general agreement in the
direction of travel and little wasted effort. There may be transport groups with very low sinuosity
that are extremely slow; one may wish to include velocity as an additional measure which
provides this information. Nevertheless, sinuosity is informative with respect to coordination and is a useful measure when considering behavioral rules that lead to coordinated transport.

**Figure 2.2:** Sinuosity is defined as the total path length (dashed line) divided by the shortest possible path (displacement; solid line). A) Path with high sinuosity. B) Path with low sinuosity.

When possible, both the rate of delivery and sinuosity should be recorded. The delivery rate provides a more comprehensive estimate of overall efficiency, while sinuosity is more directly related to coordination and is easier to measure. The most appropriate efficiency measure to use depends on the research question. While there is no inherent relationship between the rate and sinuosity, these efficiency measures should agree much of the time. A species or colony with a high average sinuosity for cooperative transport, one that takes a circuitous route back to the nest, is likely to have a relatively low delivery rate.
2.6 EFFICIENCY PARAMETERS

The literature provides an incomplete understanding of the mechanisms and behavioral rules used in cooperative transport. There are pieces of information for many species, but research has not progressed enough to give us a complete understanding of the cooperative transport process in any species. Given the disparities among species and the available information, it is difficult or impossible to draw broad conclusions about cooperative transport across species. In this section, we identify promising areas for research and we propose behavioral parameters that may modulate efficiency.

One requirement for highly efficient cooperative transport is that the group members agree on the direction to move the object. If the efforts of all workers are aimed in the same direction, transport is rapid with few deadlocks, while if workers are trying to move the object in different directions, progress is slow, likely with frequent deadlocks. The ability of a transport group to align the directions that workers are trying to move the object is an important modulator of transport efficiency. Workers may do this by forming a consensus on direction of travel.

Consensus decisions play an important role in other aspects of social insect behavior. Social insect colonies must sometimes choose a new nest location, during colony fission or budding, or because an existing nest is destroyed. This choice is a critical decision for a colony, with clear fitness consequences. Workers must agree on a location quickly, and know when an agreement has been reached. If a colony initiates relocation before a consensus is reached, the colony can split, with only a portion of workers moving to each of several sites. Decisions on nest location have been studied in *Apis mellifera* (Seeley and Visscher 2003, 2004) and *Temnothorax albipennis* (Pratt et al. 2002; Pratt 2005), among others. For both of these species, the presence of a quorum at a possible nest site is a cue that a decision has been reached (Pratt et
al. 2002; Seeley and Visscher 2003, 2004; Pratt 2005). Similarly, quorum sensing may play a role in cooperative transport.

What mechanisms do ants have for assessing consensus or quorum information about directional movement? Is information, in fact, exchanged among workers, and if so, does it pass directly via communication, or indirectly via changes in the forces acting on the food object or another mechanism? In the next subsections, we discuss potential mechanisms of information transfer and we define a new concept: persistence. Variation in persistence with respect to direction may lead to successful directional movements of the object being carried.

**Information transfer**

Based on the high degree of coordination observed in some transport groups, we hypothesize that during cooperative transport efforts information is transferred among workers. Studies of certain aspects of cooperative transport, such as size-matching of group size to prey size, suggest that information transfer occurs (Robson and Traniello 1998; Franks et al. 2001). As discussed above, work done by Franks et al. (2001) suggests that a large worker leaves a transport group if she is not needed. Perhaps these workers assess that the portion of the mass that they are carrying is low and that their effort unnecessary.

During a transport effort, the workers in the transport group are in physical contact with the item being carried. Forces exerted by workers cause vibrations and small-scale deformations in the object, transmitting information about the direction of force through the object, even if it remains stationary. Therefore, a worker might detect the forces that other workers exert on the object by observing these vibrations or deformations. This is a potential mechanism of information transfer. Consider a scenario in which there are 5 workers in a transport group, 3 of
which are pulling North, while the other two pull South. If the workers pulling south were able to
detect that the other workers are pulling north (because, for instance, they observe slight
movement or deformation to the north in moments when they pull less forcefully), they could use
that information to change their behavior. By sensing the forces of other workers on the object, a
worker could also sense a quorum with respect to direction of travel. Information gained through
this physical mechanism could inform behavioral algorithms and increase transport efficiency.
Therefore, we hypothesize that the effectiveness of a transport group in sensing forces through
the object is a parameter that modulates efficiency.

Of course, information transfer need not be via mechanical forces on the object. There are
a number of other potential mechanisms, including visual information, olfactory signals and
vibrational signals initiated by workers. Each of these sensory modes has been shown to be
important in one or more ant species (e.g. Åkesson and Wehner 2002; Steck 2012; Pielstroem
and Roces 2012). However, the physical mechanism described above – through forces on the
object being carried – is a mode of information transfer that emerges naturally from the task of
cooperative transport. It requires that workers be capable of sensing a cue (vibrations or small-
scale deformations), but does not require that workers have an adaptation for sending a signal.
Therefore, we feel experimental tests of this potential mechanism are warranted.

**Persistence**

We hypothesize that persistence modulates of efficiency. Uncoordinated transport is
characterized by many deadlocks, in which workers pull in multiple directions. In long-lasting
deadlocks, workers do not seem to change their behavior even though no progress is occurring.
We define a new way to characterize how deadlocks are resolved: persistence. Persistence is a
worker’s reluctance to giving up or to changing the direction of motion. Workers that are unlikely to change their behavior in a deadlock – regardless of the behavior of other workers– have high persistence. On the other hand, workers that respond to a deadlock by changing their behavior – for example by changing the direction they attempt to move the object or simply by giving up – have low persistence.

Inefficient ant species do not seem to alter their behavior based on what other workers in a transport group are doing, which results in uncoordinated transport (e.g. *Myrmica rubra*, *Ectatomma ruidum*; Czaczkes and Ratnieks 2013). These ants lack the ability to detect the forces of other ants, or lack the ability to act on this information. Consequently, their attempts at cooperative transport have many deadlocks and rarely succeed. Transport efforts of these species are likely to also have high sinuosity (see Figure 2.2). As discussed above, we hypothesize that highly efficient species can detect the forces of other workers and act on this information. These ant species are adept at changing their behavior based on what other workers are doing (e.g. *O. longinoda*, Wojtusiak et al. 1995), resulting in efficient transport with infrequent, short-lived deadlocks.

Persistence is an individual-level parameter that modulates transport efficiency. A transport group with low mean persistence can more quickly overcome deadlocks; as workers pulling or pushing in a direction that opposes other workers make no progress and leave or change their direction. A transport group where all workers are highly persistent pulls in opposing directions, without progress, indefinitely. Therefore, we expect groups with low average persistence to be more efficient than groups with high average persistence. Variation in persistence allows an organizational mechanism to break deadlocks, but does not ensure accuracy in direction of travel. However, changing the direction of travel can be achieved more
readily once a deadlock is broken and movement is occurring. In addition to the average persistence of a transport group, variation in persistence is also important. A group in which all members have very low persistence stochastically changes its direction many times, increasing sinuosity. On the other hand, high persistence among a small number of workers, while others are not persistent, could optimize efficiency. In that case, one would expect the overall direction of movement to be the direction of the persistent members. If persistence increases with better information about nest direction, then the one would expect the direction of movement to be generally toward the nest.

Another possibility for how persistence affects efficiency is that the persistence of workers varies over time during a deadlock or transport effort, as information about nest direction or the behavior of other workers becomes more or less available. Thus we present three hypotheses about the effect of persistence, which are not mutually exclusive: transport groups with low mean persistence are more efficient than groups with high mean persistence, variation in persistence among workers decreases the time spent in deadlocks, and variation in persistence of a single worker over time affects the contribution of that worker to the efficiency of the effort. If persistence or variation in persistence modulates the efficiency of transport efforts, the workers may still not directly detect the forces of other workers. Feedback of any kind, including workers simply noticing that the food is not moving, could result in persistence modulating efficiency. We also note that if a worker does not change her behavior based on the behavior of others in the group, it is either because she is very persistent, or because she is simply unable to detect the behavior and direction preference of the other workers. Disentangling whether workers are “stubborn” because of high persistence or because they lack information will be challenging.
Nevertheless, investigating persistence will advance our understanding of the behavioral rules that lead to efficient transport.

2.7 CHALLENGES AND SYNTHESIS

One challenge associated with studying coordination in cooperative transport involves information transfer. This transfer can occur through direct communication or another mechanism. There is no direct evidence that workers in transport groups are communicating during a transport effort, yet as discussed above, the ability to transfer information within a transport group, for instance about direction of travel, improves transport efficiency. Some studies have supported the idea that information transfer is occurring. As discussed above, groups of *F. incerta* fail to transport an item to the nest when the scout is removed, even if there are sufficient workers at the food item (Robson and Traniello 2002). Why would this be the case if there were not the transfer of necessary information from the scout to the group? Of course there are other possible explanations, but we should not rule out information sharing simply because we have not directly observed it. The challenge is that measuring communication or any other mode of information transfer occurring between workers in a transport group is difficult. For example, if workers were communicating chemically, as they do in other contexts, collecting the chemical signals during ongoing transports would be challenging.

Although mechanisms of information transfer are often unobservable, explicit tests of potential mechanisms can be practical. In the previous subsection, we discussed forces as a potential mechanism of information transfer. This hypothesis can be tested by applying appropriate external forces to the object during a transport effort. Testing the importance of more direct communication modes, such as chemical signals, is more difficult, but these tests are
possible in some cases. For example, one could test if vibrational or auditory communication is occurring by altering the ability of certain workers to sense those signals.

Another major challenge in cooperative transport research involves identifying and testing behavioral algorithms. As outlined above, we have made some progress in characterizing aspects of cooperative transport in particular species. Some of these studies have looked at circumstances that lead to more efficient transport (see Transport section – e.g. turning in *P. oxyops*, taking turns with heavy loads in *G. sulcata*, etc.). However, very few studies have attempted to ascertain the behavioral mechanisms that lead to these efficient circumstances. While *G. sulcata* workers take turns with heavy loads, increasing efficiency (Daly-Schweitzer et al. 2007), the authors proposed no behavioral rules leading to this rotation behavior. Franks (1986) suggested a behavioral rule regarding cooperative transport in *E. burchellii*, namely, that once a large worker has begun to move an item, additional smaller works join until the speed of transport matches the speed of the surrounding column. Testing this type of behavioral algorithm will dramatically improve our understanding of cooperative transport.

One reason tests of behavioral algorithms are largely missing from the literature is that explicitly identifying and testing behavioral algorithms is difficult. Behavioral rules cannot be directly observed; one can only experimentally test the consequences of such rules. Multiple rules can have similar consequences; disentangling these rules poses an additional challenge. We suggest overcoming these challenges with a two-stage approach: 1) use simulations (e.g. individual-based models) to identify rules that are supported in a theoretical context, then 2) test those rules experimentally. Here, we discuss examples of successful studies using each of these stages.
Computational models and simulations play an important role in our understanding of the dynamics of biological systems. Simulations can be particularly effective when studying complex systems like collective behavior, and have often been used in this field (Sumpter 2010). By simulating group behavior under different individual parameters, Couzin et al. (2002) developed strongly supported hypotheses for behavioral rules for group movement, such as fish schooling. Couzin et al. (2002) assigned two simple rules that apply to individuals: 1) there is a minimum distance that individuals keep between themselves and others and 2) beyond that distance individuals are attracted to others and tend to orient themselves in the same direction as others. Simulations of groups of individuals with these rules exhibited several modes of group behavior, depending on the distances over which each rule was applied (Couzin et al. 2002). Groups with individuals that orient to others over a relatively small radius form a torus, so that the group rotates around an empty center. A larger “zone of orientation” results in a flock or swarm, in which all individuals are aligned in the same direction (Couzin et al. 2002). Both of these modes of behavior are observed in nature, in birds and/or fish (Couzin et al. 2002), which supports the hypothesis that the behavioral rules used for the simulation are found in nature as well. This is just one example of a simulation that was used to identify likely behavioral algorithms.

Once a theoretically sound behavioral rule has been identified, the nature of the proposed rule might suggest a specific experiment to falsify or support it. While not related to cooperative transport, Wittlinger et al. provides an excellent example of an experimental test of a behavioral algorithm in ants. Wittlinger et al. (2006) tested a behavioral rule regarding navigation in *Cataglyphis fortis*. The putative rule was that workers use a “step integrator” to keep track of the number of steps they take on a trip away from the nest, and take approximately the same number
of steps on the return trip to successfully find the nest. A consequence of this rule is that the navigation fails if step-size is altered before the return trip. Wittlinger et al. (2006) tested the proposed behavioral rule by experimentally testing that consequence. Step-size is determined by leg-length; therefore, Wittlinger et al. (2006) experimentally lengthened the legs of some foraging workers while shortening others. On the return trip, the workers with shorter legs did not travel far enough, while those with longer legs travelled too far and overshot the nest (Wittlinger et al. 2006). The experiment supported their hypothesis and is a useful template for other tests of behavioral rules.

There is wide variation in ant species’ cooperative transport efficiency. Understanding the behavioral rules that allow efficient transport to emerge will greatly increase our understanding of collective behavior. In an effort to stimulate research into proximate mechanisms associated with cooperative transport, we have synthesized past research on such mechanisms of cooperation and suggested future research topics. In this review we propose quantitative measures of transport efficiency, which will allow for direct comparisons of transport ability between species. Categorizing a large number of ant species using these efficiency measures, in concert with the categories defined by Czaczkes and Ratnieks (2013), will clarify much of the evolutionary history of this behavior. We present a flowchart showing the phases of transport as well as the flow of information. This flow chart facilitates careful modeling of transport efforts. We define two behavioral parameters that are hypothesized to modulate transport efficiency: information transfer and persistence. Understanding how these parameters affect efficiency will elucidate behavioral algorithms workers use during transport. We have also tried to address some of the challenges associated with research into proximate
mechanisms of cooperation. Cooperative transport is a fascinating behavior that, in efficient cases, requires a high degree of coordination; at a minimum workers must agree on direction of travel. Our understanding of this behavior will benefit from more research as outlined in this review.
CHAPTER 3

Object mass and size affect group speed and coordination time, but not maintenance of coordination, during cooperative transport in *Paratrechina longicornis* ants

3.1 ABSTRACT

Some ant species cooperatively transport a wide range of extremely large, heavy food objects of differing shapes and materials. It is reasonable to expect the nature of each object, its mass and size, for example, to have potentially dramatic effects on the success of the transport attempt. While previous studies have examined how object mass and size affects the recruitment of additional workers, less is understood about how these attributes affect groups’ organization and the transport itself. I hypothesized that heavier and larger objects each require more ants carrying them, and that if each ant must bear a heavier load (higher mass per ant), coordination time (the time it took for the group to begin movement), sinuosity (coordination during movement), and speed should all be negatively affected. Object size may also affect these results metrics separately from mass. Using the ant *Paratrechina longicornis* as a study system, I presented groups of ants with baits of the same material and shape, but varying sizes and masses, and I recorded the ants’ transport attempts. For each trial, I measured the number ants involved (group size), coordination time, sinuosity, and the speed of the transport group. As I expected, heavier baits required larger groups to begin movement, and larger objects of a given mass also required larger groups. Baits with higher mass per ant took longer to begin movement, and this effect was stronger for larger disks. Baits with higher mass per ant also had substantially lower speed, but contrary to the coordination time results, this effect was lessened for large objects. Finally, contrary to my hypothesis, sinuosity was not affected by any of the parameters I examined, as *P. longicornis* groups move in relatively straight lines regardless of the object they are carrying. For
a given group size, objects that are heavier take longer to move and move more slowly. Object size, on the other hand, negatively affected coordination time, but positively affected speed. These results fill a gap in our understanding of cooperative transport and suggest new hypotheses about how group size may affect coordination.

3.2 INTRODUCTION

Cooperative transport is a highly conspicuous example of emergent group behavior in ants, and as such, has been the subject of numerous studies over the past several decades (Berman et al. 2011; Czaczkes and Ratnieks 2013; McCreery and Breed 2014). Groups of ants attempting to move a large object together must overcome several challenges. Once a sufficient number of workers have assembled in the vicinity of the object, they must make a collective decision about travel direction to align their forces, and then maintain consensus while navigating through a complex, heterogeneous environment to their nest (McCreery and Breed 2014). Workers from many species of ant fail to overcome these challenges (Moffett 2010; Czaczkes and Ratnieks 2013), yet in some species, worker groups are capable of transporting a wide range of extremely large, heavy objects of diverse shapes and materials (Wojtusiak et al. 1995; Czaczkes and Ratnieks 2013; McCreery and Breed 2014).

Despite the growing scientific interest in cooperative transport (McCreery and Breed 2014), we have only a partial understanding of how group behavior interacts with properties of the object being carried, such as size and mass. These effects have been most closely examined during the recruitment phase of cooperative transport; for a few species we know, for example, that heavier objects elicit the recruitment of more workers from the nest (Detrain and Deneubourg 1997; Cogni and Oliveira 2004; Daly-Schveitzer et al. 2007; Cerda et al. 2009).
With respect to post-recruitment behavior – i.e. organization and transport – our understanding of the implications of object properties is largely limited to observations of the distributions of sizes and masses of objects typically carried by groups (Traniello and Beshers 1991). These studies provide valuable insight into the function of cooperative transport in natural settings, but cannot satisfactorily inform how object properties affect group behavior and success, because only certain kinds of objects are naturally available in a given location – e.g. large heavy objects and small, lighter objects may be available, but perhaps not small, heavy objects. Natural bait objects also differ in myriad, potentially confounding, ways. We do know that in some species group size (the number of ants involved in the transport) is correlated with object mass (Robson and Traniello 1998; Franks et al. 2001), but these experiments did not isolate the effect of mass from other attributes, like size.

On the other hand, for experiments focusing on the mechanisms of cooperative transport, particularly on the organization and transport phases, researchers have necessarily provided groups with baits that are uniform or essentially uniform (Berman et al. 2011; Kumar et al. 2013; Gelblum et al. 2015; Buffin and Pratt 2016; McCreery et al. 2016b). These studies provide us with substantial information about the mechanisms of cooperative transport in several species, but are less informative about the effects of object properties. In summary, researchers have generally either observed ants carrying natural objects that differ in many confounding ways, or have provided ants with identical objects. No studies of cooperative transport have examined the effect of object properties on group coordination and transport by providing groups with baits differing in size or mass while keeping other properties constant.

Isolating the effects of object size and mass from other object properties allows exploration of several interesting questions (see Table 3.1). For example, is group size more
Table 3.1: Hypothesis table. Includes expected effects of possible predictors on responses, as well as rationale for hypotheses. Response variables include group size and the following success measures: coordination time, sinuosity, and speed. Possible predictors include object size and object mass (for group size response) or object mass per ant (for success measures). I could not separately evaluate the effect of object mass and group size on success measures, as these predictors were correlated (see results).

<table>
<thead>
<tr>
<th>Response</th>
<th>Hypothesized effects of possible predictors</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group Size</strong></td>
<td></td>
</tr>
<tr>
<td>Object mass</td>
<td>Positive effect. Heavier objects should require larger groups to move them.</td>
</tr>
<tr>
<td>Object size</td>
<td>Positive effect. Larger objects can fit more ants, and may require more ants due to object stability.</td>
</tr>
<tr>
<td><strong>Object mass per ant</strong></td>
<td></td>
</tr>
<tr>
<td>Coordination time</td>
<td>Positive effect. If each ant must carry a heavier load, it may take longer for groups to align forces and coordinate.</td>
</tr>
<tr>
<td>Object size</td>
<td>Positive or negative effect. Stability issues may slow down coordination. If larger objects also have larger groups, these groups may require more time to coordinate. Alternatively, large groups may coordinate quickly as they are less affected by transient individual decisions.</td>
</tr>
<tr>
<td>Sinuosity (maintenance of coordination)</td>
<td>Positive effect (higher mass per ant lowers coordination maintenance). Groups in which each ant carries a heavier load may stop and start, leading to direction changes.</td>
</tr>
<tr>
<td>Object size</td>
<td>Positive or negative effect. Stability issues may require more stops and starts, increasing sinuosity. If larger objects also have larger groups, these groups may start and stop more often, or may have improved coordination (see above).</td>
</tr>
<tr>
<td>Speed (displacement over time for whole trial)</td>
<td>Negative effect. Groups in which each ant carries a heavier load should move slower than an unburdened walking speed. If these groups have higher sinuosity, this will also decrease speed for the trial.</td>
</tr>
<tr>
<td>Object size</td>
<td>Positive or negative effect. Stability issues may slow down groups carrying large objects. If large objects have larger groups, these groups may have higher or lower instantaneous speed, depending on the effect of group size on coordination (see above). If object size affects sinuosity, this should also affect overall speed for the trial.</td>
</tr>
</tbody>
</table>

influenced by object mass or size? One expects heavier objects to require more workers for carrying, however, object size may affect the stability of the group, so more individuals may be needed to carry a large object even if it is light. Larger objects have more gripping points, so the maximum group size is likely to be larger. Thus, for a given weight, larger objects may be easier to carry, and we may expect higher speeds or more rapid coordination. This relates to the
question of how group size affects coordination and transport. Previous research has shown that, in *Paratrechina longicornis*, or long-horn crazy ants, transport groups with more workers move at higher speeds than smaller groups (Gelblum et al. 2015; McCreery et al. 2016b), though this is not true of army ant groups (Franks et al. 1999). Group size also likely affects coordination. Intuitively, one might expect a collective decision about travel direction to be more difficult among 30 individuals than 3, so it could be predicted that groups with more ants would take longer to begin moving. On the other hand, small groups may be more affected by transient individual decisions, and theoretical work predicts that large groups will coordinate their efforts more quickly (McCreery et al. 2016a). Object mass may, of course, interact with group size, and mass per ant is a natural variable to examine in this context. It is intuitive that if each ant must carry a heavier load (higher mass per ant), transport may be more difficult, with lower speeds and potentially less coordination. Isolating the effects of object size and mass allows tests of these hypotheses (Table 3.1).

Here, I explored the effects of object size and mass using *P. longicornis*, a species that excels at cooperative transport (Gelblum et al. 2015; McCreery et al. 2016b). I provided *P. longicornis* colonies with uniform objects of different weights and sizes to discover how these variables affect group size, and I was particularly interested in affects on three measures of group success during transport: coordination time (time to begin movement), sinuosity (coordination during movement), and speed. I hypothesized that object mass and size would each affect group size, that heavier and larger objects require more ants (Table 3.1). While I did not directly control group size, I also analyze how group size affects the other response metrics. Thus, I also hypothesize that trials in which each ant was carrying a heavier load (higher mass per ant) would have longer coordination times, higher sinuosity (lower coordination), and lower speeds.)
Hypotheses and rationale are included in Table 3.1. Understanding how object size and mass affect transport success is key to understanding the mechanisms of cooperative transport.

3.3 METHODS

Experiments

To disentangle the effects of size and weight of objects, I provided *P. longicornis* colonies with baits, described below, that differed only in size and weight, with a large weight range in baits of a given size. For each trial, I video recorded groups of workers as they began transporting each bait to their nest. I conducted experiments in the field, using sites adjacent to six different *P. longicornis* colonies located at the Arizona State University campus in Tempe, Arizona. I set up trials only on smooth, flat surfaces (such as concrete) near a single nest entrance, so that all recruited workers had the same goal. I taped white paper to the ground, which I replaced between each trial, to remove any possible effects of pheromones on subsequent trials. I placed a large cricket (earlier killed by freezing) on the paper, to elicit a strong recruitment response from workers. I waited to begin each trial until a group was successfully moving this cricket, to ensure that there were sufficient workers in close proximity to my bait. This allowed me to measure the time it took groups to coordinate, without the potentially confounding influence of recruitment time. When the cricket was moving successfully, I replaced it with one of the experimental baits, discussed below. Baits were not reused between trials. I video recorded all trials using an Apple iPod touch, which provides excellent focus at short focal lengths, on a purpose-made stabilizing support. Each trial ended when the group left the video frame.
Baits

Baits were disks, constructed from rigid craft foam. To make baits attractive to the ants, I applied a uniform volume of tuna-permeated oil to the circumference of each bait; oil came from cans of tuna packed in olive oil. Tuna is a common ant bait that elicits group transport behavior in *P. longicornis* (McCreery et al. 2016b). Baits were allowed to dry before use, and always elicited enthusiastic transport attempts from *P. longicornis* workers. Diameters of baits ranged from 1.29 to 2.44 cm, and weights ranged from 34 to 825 mg. I altered the weight of baits by gluing one or more objects on top of the disks, such as plastic beads, small metal washers, and small metal nuts. I also added an ID tag to each bait, which I tracked during video analysis. Summary statistics for the baits, categorized into three size classes, are included in Table 3.2. While I was not able to make the largest disks as light as the lightest small disks, nor the smallest disks as heavy as the heaviest large, I included a large range in weight within each size class, as shown in Figure 3.1A. Photos of examples of baits are shown in Figures 3.1B and 3.1C.

**Table 3.2:** Summary statistics for baits in each size class.

<table>
<thead>
<tr>
<th>Size class (sample size)</th>
<th>Mean diameter in cm (s.e.)</th>
<th>Mean mass in mg (s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small (19)</td>
<td>1.57 (0.029)</td>
<td>98 (16)</td>
</tr>
<tr>
<td>Medium (20)</td>
<td>1.93 (0.020)</td>
<td>264 (48)</td>
</tr>
<tr>
<td>Large (23)</td>
<td>2.23 (0.017)</td>
<td>310 (37)</td>
</tr>
</tbody>
</table>
Figure 3.1: Bait information and examples. a) Bait weights for each size class. b) Examples of baits. c) *P. longicornis* workers transporting bait.

Data extraction

I extracted several kinds of data from the videos, by first recording the location of the bait over time. For each video, the location and orientation of the bait was manually recorded every second using Matlab. I tracked the location of the ID tag on the bait, and converted this trajectory to the trajectory of the center of the disk. This provides the trajectory of the group rather than of individual ants. I used this trajectory information to measure coordination time, speed, and sinuosity (the ratio of path length to displacement). I defined coordination time as the time it took the group to move the bait 1 cm. At this time, all groups were successfully moving
smoothly, whereas distances on the order of 1 mm were sometimes reached haltingly. I also measured sinuosity, which is the total path length divided by the displacement. Paths with lower sinuosity indicate more coordinated groups. Finally, I measured speed as the displacement of the group for the whole trial (rather than path length) divided by the elapsed time since the group had moved 1 cm. Thus coordination time is not included in the speed measurement.

In addition to these results metrics that I measured from group trajectories, I manually measured the group size that was necessary for successful movement. To find this, I counted the number of ants attached to the bait in the video frame in which the group had just moved 1 cm. I explored whether object mass and size affect group size, and I also examined the effect of group size on other response variables.

Statistical analyses

All statistical analyses were performed in R, version 3.2.2 (R Core Team 2015). I first explored the data visually to identify correlated predictors that it would be inappropriate to incorporate together in the same model. I used linear mixed-effects models on log-transformed response variables to identify important predictors for each variable of interest. Log transformation of response variables was sufficient to meet assumptions of normality. For all models, I included colony as a random effect acting on the intercept. Each of my full models incorporated two possible predictors, and I used AICc to select the best among possible models. Like AIC, AICc reflects likelihood with a penalty for model complexity. AICc has a correction for small sample sizes, but is also appropriate to use for larger samples, as it converges to AIC. I did not feel it was appropriate to examine possible interactions only while also including the main effects associated with the interaction, as in this project it is intuitive that interactions may
effect responses without main effects. For example, it is reasonable to expect the interaction between object size and group size to impact efficiency without each of those factors separately doing so. I included a model with no predictors as a possible model for each response variable, to see if models with the predictors I observed perform better than a null model. Any models with ΔAICc values less than 2 I considered to be statistically indistinguishable from the best model. Because of a fairly strong correlation between mass and group size (see results), I did not include both mass and group size as possible predictors in other models. Instead, I combined these variables into a single predictor, mass per ant. It is intuitive that mass per ant may affect cooperative transport. Object size is a continuous variable in my models (measured as the diameter of each disk), but for clarity, in some figures I have categorized sizes into small, medium, and large.

3.4 RESULTS

1) Group size

Object mass and group size at the point the group had moved 1 cm were strongly correlated (Figure 3.2A); heavier objects require more ants to move them. This effect is reflected in the best model for group size, which includes a positive effect of object mass (Table 3.3). Larger-sized objects also tended to be carried by larger groups (Figure 3.2B). While this effect was smaller, it is also reflected in the best-fit model. Using AICc, this model was not distinguishable (ΔAICc < 2) from the model including object diameter and the interaction between mass and diameter, which reports that larger objects require more ants, and this effect is heightened for heavier objects. However, the conclusions from this alternative model are essentially the same. Both models include significant, positive effects of both size and mass, in
one case through two main effects, in the other through a main effect substantially modified by an interaction.

**Figure 3.2:** Effect on group size of a) object mass and b) object size. Group size is positively affected by both mass and object size. Sample size = 62.

**Table 3.3:** Results of model selection for group size. Models were evaluated using log(group size) to meet assumptions of normality. Models listed above the bold line are indistinguishable by AICc. Sample size = 62, and degrees of freedom ranged from 53 to 56 for all models.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Coefficients (F-values)</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mass</td>
<td>Size</td>
</tr>
<tr>
<td>Mass + Diameter</td>
<td>1.8*** (69.0)</td>
<td>0.53*** (13.9)</td>
</tr>
<tr>
<td>Diameter + Mass:Diameter</td>
<td>-</td>
<td>0.39* (6.7)</td>
</tr>
<tr>
<td>Mass + Diameter + Mass:Diameter</td>
<td>1.26 (0.38)</td>
<td>0.49* (5.1)</td>
</tr>
<tr>
<td>Mass:Diameter</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mass + Mass:Diameter</td>
<td>-1.96 (1.68)</td>
<td>-</td>
</tr>
<tr>
<td>Mass</td>
<td>2.25*** (106)</td>
<td>-</td>
</tr>
<tr>
<td>Diameter</td>
<td>-</td>
<td>1.10*** (35.6)</td>
</tr>
<tr>
<td>1 (Null model)</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
2) Coordination time

Using model selection, several models predict the time it takes groups to coordinate equally well. There are four models with ΔAICc less than 2; all of these models include significant effects of both mass per ant and object size as either main effects or as part of an interaction (Table 3.4). These models all are substantially better predictors of coordination time than the models that include either only mass per ant or only object size, and are also substantially better predictors than a null model. Heavier objects, per ant, take longer for groups to move, and this effect seems to be stronger for larger objects. The effects of mass per ant and object size on coordination time do not appear to be strong, and there is substantial variation in coordination time not explained by these predictors (Figure 3.3), but especially at higher masses per ant very short coordination times do not occur.

Table 3.4: Results of model selection for coordination time. Models were evaluated using log(time) to meet assumptions of normality. Models listed above the bold line are indistinguishable by AICc. Sample size = 62, and degrees of freedom ranged from 53 to 56 for all models.

<table>
<thead>
<tr>
<th>Predictors (all models also included a random effect of colony on the intercept)</th>
<th>Coefficients (F-value)</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mass per ant</td>
<td>Size</td>
</tr>
<tr>
<td>Mass per ant + Diameter</td>
<td>63*** (13.8)</td>
<td>1.4** (8.52)</td>
</tr>
<tr>
<td>Diameter + Mass per ant:Diameter</td>
<td>-</td>
<td>0.84 (2.45)</td>
</tr>
<tr>
<td>Mass per ant:Diameter</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mass per Ant + Mass per ant:Diameter</td>
<td>-64.1 (1.38)</td>
<td>-</td>
</tr>
<tr>
<td>Mass per ant + Diameter + Mass per ant: Diameter</td>
<td>47.7 (0.173)</td>
<td>1.26 (1.22)</td>
</tr>
<tr>
<td>Mass per ant</td>
<td>74.1*** (17.6)</td>
<td>-</td>
</tr>
<tr>
<td>Diameter</td>
<td>-</td>
<td>1.74** (11.6)</td>
</tr>
<tr>
<td>1 (Null model)</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 3.3: Effect of a) mass per ant (object mass divided by group size) and b) object size on coordination time of groups. Mass per ant and object size both have positive effects on coordination time, though these effects are not very strong. Sample size = 62.

3) Sinuosity

Sinuosity is not strongly affected by either mass per ant or by object size (Figure 3.4, Table 3.5). Models with ΔAICc less than 2 include 1) the interaction between mass per ant and object size or 2) mass per ant as a main effect alone. However, the null model, including no predictors, is also indistinguishable from these models. None of the variables I manipulated in my experiments had a substantial effect on sinuosity, which was low (indicating high efficiency) in all trials, with relatively low variation.
Figure 3.4: The effect on group sinuosity of a) object mass per ant and b) object size. High sinuosity indicates low coordination during transport. Neither mass per ant nor object size substantially impacted sinuosity, and models with these predictors do not improve prediction over a null model. Sample size = 62.

Table 3.5: Results of model selection for sinuosity. Models were evaluated using log(sinuosity) to meet assumptions of normality. Models listed above the bold line are indistinguishable by AICc. Sample size = 62, and degrees of freedom ranged from 53 to 56 for all models.
4) Speed

Speed was measured as the displacement of the object during the whole trial, divided by the time that elapsed since the group moved 1 cm. I could not distinguish a single best model for speed using ΔAICc, as 4 different models had ΔAICc values less than 2 (Table 3.6). These models all included effects of both mass per ant and object diameter either as main effects or within an interaction. Speed was strongly and significantly correlated with mass per ant (Figure 3.5A, Table 3.6), and the model including object diameter without mass was a very poor predictor of speed. Object size seems to also be a significant predictor of speed (Figure 3.5B), but has a relatively small effect; the model including mass per ant without object size performed nearly as well as other models (ΔAICc = 2.1). Interestingly, three of the four best-performing models include a negative interaction between mass per ant and object size, and even the model including only this interaction performs well. This indicates that the effect of mass per ant is smaller for larger objects. In other words, while there is a strong negative association between mass per ant and speed, this association is lessened for larger objects. This effect is difficult to detect visually, but for baits with similar masses per ant (e.g. purple points in Figure 3.5B), larger baits were transported with moderately higher speed.
Table 3.6: Results of model selection for speed. Models were evaluated using log(speed) to meet assumptions of normality. Models listed above the bold line are indistinguishable by AICc. Sample size = 62, and degrees of freedom ranged from 53 to 56 for all models.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Coefficients (F-values)</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>(all models also included a random effect of colony on the intercept)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mass per ant:Diameter</td>
<td>-</td>
<td>-35.2*** (117)</td>
</tr>
<tr>
<td>Mass per ant + Mass per ant:Diameter</td>
<td>-30.4 (1.94)</td>
<td>-21.3 (4.16)</td>
</tr>
<tr>
<td>Mass per ant + Diameter</td>
<td>-69.6*** (101.4)</td>
<td>-0.37 (3.71)</td>
</tr>
<tr>
<td>Diameter + Mass per ant:Diameter</td>
<td>-</td>
<td>0.25 (1.28)</td>
</tr>
<tr>
<td>Mass per ant</td>
<td>-72.7*** (111)</td>
<td>-</td>
</tr>
<tr>
<td>Mass per ant + Diameter + Mass per ant:Diameter</td>
<td>-38.3 (0.684)</td>
<td>-0.09 (0.0377)</td>
</tr>
<tr>
<td>Diameter</td>
<td>-</td>
<td>-0.82* (7.19)</td>
</tr>
<tr>
<td>1 (Null model)</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Figure 3.5: The effect of a) object mass per ant and b) object size on group speed. Objects with higher mass per ant are moved more slowly, and this effect is somewhat lessened for larger objects.
3.5 DISCUSSION

The mass and size of an object should affect how groups of ants cooperatively transport that object, and may have important implications for the mechanisms of coordination and transport. However, previous research has not isolated these properties to carefully examine how they impact group behavior. I found that object mass and size impact important aspects of group transport. Some of these results were intuitive and unsurprising, while others were less predictable, and suggest interesting new hypotheses.

I first examined object properties’ effects on the group size necessary to begin movement – i.e. the group size when the object had moved 1 cm. Supporting my hypothesis, I found that heavier objects require more ants to move them. This also fits with previous research showing that in several species more ants are recruited to larger objects for cooperative transport (Detrain and Deneubourg 1997; Cogni and Oliveira 2004; Daly-Schweitzer et al. 2007; Cerda et al. 2009). The association between mass and group size was quite strong (Figure 3.2A), but by itself, mass could not adequately account for the variation in group size. Object size was also important, and for a given mass, larger objects tended to be carried by larger groups. This is intuitive, as more workers can fit around larger objects, but the results indicate more than this. For these larger objects, groups were not able to successfully begin movement unless group size was high enough. Rather than being attributable only to more space being available, this shows that larger groups are in fact required. This may be due to object stability. If groups attempt to lift objects they carry, larger objects being lifted only from one side would require more torque than smaller objects. Thus, larger objects may require a more even distribution of workers around the object, which is more easily achieved with larger groups. This potential effect could be directly tested in
the future by controlling the distribution of ants around objects, by constructing unbalanced objects, or objects that can only be gripped on one side, for example.

I was particularly interested in three measures of group success during transport: coordination time, sinuosity, and speed. I hypothesized that each of these success measures would be negatively impacted by mass per ant, and I also expected possible effects of object size (Table 3.1). My hypotheses were partially supported, but these measures responded differently to the possible predictors. Both mass per ant and object size affected coordination time. When each ant must carry more mass groups take longer to coordinate, and this effect seems to be exacerbated by larger object sizes, perhaps reflecting the possible stability issues with larger objects discussed above. If workers must be more evenly distributed around larger objects, it is intuitive that it may take longer for coordination to be achieved. However, there is substantial variation in coordination time that my predictors cannot account for (Figure 3.3). This suggests that factors that I did not evaluate, such as individual group members’ identity and behavior, may also be important for determining the time it takes groups to coordinate. Indeed, other research also indicates that individual behavior affects group coordination during cooperative transport (see Chapter 5).

Unlike coordination time, group sinuosity was not substantially affected by any of the object properties I examined. Sinuosity is one measure of group coordination after movement begins. Uncoordinated groups may change directions frequently leading to relatively high sinuosity. *P. longicornis* groups seem to always move in nearly straight lines, with low sinuosity, indicating that these groups excel at maintaining coordination once it is achieved (McCreery et al. 2016b). Contrary to my hypothesis, while the time it takes to coordinate is affected by the mass of the object, per ant, and by object size, these things do not affect the maintenance of
coordination, at least not in a way that leads to groups changing direction more. It would be interesting to know if less coordinated cooperative transporters with higher sinuousities in their transport attempts are affected more by object properties.

Of the success measures I examined, group speed was affected most strongly by my predictors. Fitting my hypothesis (Table 3.1), speed was strongly associated with mass per ant. For a given group size, as objects become heavier, the group moves substantially more slowly. However, object size also affected speed, and for a given mass per ant, larger objects were actually transported slightly faster than smaller ones. This is the opposite of the effect I observed for coordination time. While ants may take longer to begin moving larger objects, they seem to move them faster after that point. Both of these effects may relate to group size. I could not isolate the impact of group size on result metrics – due to the correlation with object mass – but larger objects tended to be carried by larger groups. Considering, then, that larger objects have larger groups, it will take longer for these groups to assemble on the object and to achieve the even distribution that may be required for larger objects, leading to high coordination time. However, once objects are moving, my results indicate that these larger groups may move faster than smaller groups, even for a given mass per ant. This fits the general pattern found in previous studies of *P. longicornis* using uniform baits, that larger groups move more quickly (Gelblum et al. 2015; McCreery et al. 2016b). Perhaps larger groups are less affected by transient individual decisions – if a single ant decides to begin pulling against the direction of movement, this will impact a larger group less than a smaller group. This idea is supported in a theoretical context (McCreery et al. 2016a), which focused on coordination during the initial decision regarding travel direction. My results do not support this for this initial coordination time, but may support this possible effect on group speed. Future work should examine this more closely by isolating
possible effects of group size from object size, and by looking at the effect of the distribution of ants around an object.

Interestingly, I found that object mass and size affect coordination time and speed, but not the maintenance of coordination after transport begins (sinuosity). *P. longicornis* groups excel at moving in relatively straight lines – indicating high coordination – regardless of these factors. Larger objects require longer coordination times, but for a given mass per ant, larger objects actually move slightly faster than smaller ones. I also found, unsurprisingly, that heavier objects are carried by larger groups, and groups transporting objects with higher masses per ant take longer to begin transport, and move substantially more slowly. Separately from mass, larger objects tend to be carried by larger groups. Previous studies of the organization and transport phases of cooperative transport have either observed the natural variation of transported objects (Traniello and Beshers 1991; Robson and Traniello 1998; Franks et al. 2001) – with size and mass typically confounded – or have examined transport more mechanistically with identical objects (Berman et al. 2011; Kumar et al. 2013; Gelblum et al. 2015; Buffin and Pratt 2016; McCreery et al. 2016b). To my knowledge, this was the first study to systematically isolate the effects of object properties by varying only those properties. These findings contribute to our understanding of group behavior during cooperative transport in *P. longicornis*, and suggest new hypotheses about worker distribution and object stability. It would be valuable to examine how object properties affect cooperative transport in other species, to see if these conclusions are generalizable.
CHAPTER 4

Consensus or deadlock? Consequences of simple behavioral rules for coordination in group decisions

4.1 ABSTRACT

Coordinated collective behaviors often emerge from simple rules governing the interactions of individuals in groups. We model mechanisms of coordination among ants during cooperative transport, a challenging task that requires a consensus on travel direction. Our goal is to determine whether groups following simple behavioral rules can reach a consensus using minimal information. Using deterministic and stochastic models, we investigate behavioral factors that affect coordination. We define and investigate three types of behavioral rules governing individual behavior that differ in the information available: individuals either 1) have no information, 2) can measure transport success, or 3) measure success while also knowing whether they are aligned with the majority. We find that groups break deadlocks only if individuals more readily give up when they are going against the majority, corresponding to rule type 3 – such groups are “informed.” These behavioral rules succeed through positive and negative feedbacks that are implemented in our model via a single mechanism: individuals only need to measure the relative group sizes to make effective decisions. We also find that groups reach consensus more quickly if they have either a shared bias, high sensitivity to group behavior, or finely tuned persistence. Each of these is a potential adaptation for efficient cooperative transport. This flexibility makes the behavioral rules in the informed case relatively robust to deficiencies in the individuals’ capabilities. While inspired by ants, our results are

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2This paper was published in *PLOS One* with Nikolaus Correll, Michael D. Breed, and Samuel Flaxman.
generalizable to other collective decisions with deadlocks, and demonstrate that groups of behaviorally simple individuals with no memory and extremely limited information can break symmetry and reach a consensus in a decision between two equal options.

4.2 INTRODUCTION

Across organizational scales, the patterns and complexity of many biological systems emerge from groups of individuals obeying relatively simple rules, often without a leader (Camazine et al. 2001). Rules typically apply to individuals interacting with their neighbors, and exploit positive and/or negative feedback mechanisms leading to coordinated group dynamics (Camazine et al. 2001). Rules do not have to be simple, but if robust, efficient coordination is possible with simple rules, there is no need for complex individual behaviors to evolve. Interest in discovering rules for collective behavior has produced a rich literature, and there has been particular interest in group decision making (Couzin et al. 2005; Conradt and Roper 2005; Sumpter et al. 2012; Zabzina et al. 2014). This includes nest-site selection decisions in honeybees and *Temnothorax* ants (Visscher 2007; Seeley 2010; Sasaki and Pratt 2011; Seeley et al. 2012b), decisions by groups of neurons in brains (Marshall et al. 2009), decisions in non-neuronal organisms (Reid et al. 2015a), and more. Ant colonies are particularly well suited to studies of collective behavior because workers can be easily observed and manipulated, and indeed, pheromone trail formation in ants is a classic study system for self-organized decision making (e.g. Camazine et al. 2001; Czaczkes et al. 2015b).

In collective decisions, groups that deadlock – having approximately equal numbers of individuals aligned with each choice – fail to form consensus. This can result in a split decision, or no decision at all. For some types of decisions this can be catastrophic, and there are
behavioral mechanisms to prevent deadlocks in these cases. For example, split decisions during nest-site selection in honey bees can result in colony death (Lindauer 1955; Seeley 2010), and the “stop signal” has evolved to prevent such splits (Niven 2012; Seeley et al. 2012b; Pais et al. 2013). This stop signal is a negative feedback mechanism and, along with a positive feedback mechanism (advertising), ensures that colonies can break deadlocks to choose a single nest site (Pais et al. 2013). In fact, colonies can choose a single site even when the options are of equal quality; this is an example of symmetry breaking. A substantial body of research has focused on symmetry breaking in various taxa including honey bees, ants, cockroaches, and more (e.g. Deneubourg et al.; Vries and Biesmeijer 2002; Sumpter 2010; Hamann et al. 2010; Seeley et al. 2012b). Symmetry among choices makes deadlocks more likely, and the ability to overcome deadlocks is a crucial component of any collective decision in which a group must choose a single option.

A collective decision that is particularly prone to deadlocks occurs during cooperative transport in ants. Cooperative transport is the movement of large objects such as food items, intact, by multiple individuals (McCreery and Breed 2014), and it requires making one or more decisions about travel direction. Workers of some ant species collaborate to carry objects many thousands of times their mass (Hölldobler et al. 1978; Wojtusiak et al. 1995; Franks et al. 1999; Berman et al. 2011; Czaczkes and Ratnieks 2013). This requires a high degree of coordination across many individuals, and ant species vary substantially in their ability to coordinate. Some species move objects rapidly toward their nests, while others are categorized as uncoordinated, having many deadlocks, with workers pulling in opposing directions for minutes or hours (Moffett 2010; Czaczkes and Ratnieks 2013). Even in species with efficient cooperative transport, short-lived deadlocks occur (Berman et al. 2011; Czaczkes and Ratnieks 2013).
Deadlocks may happen if individuals have conflicting information about the direction of the nest, or if the group encounters an obstacle blocking the nest direction, requiring a new decision.

Deadlocks may be more likely in cooperative transport than other decisions because cooperative transport groups are often relatively small. Larger groups are less affected by the behavior of single individuals. Split decisions are impossible in cooperative transport because group members are physically tethered together by the object they are attempting to carry, so deadlocked groups are stuck. Thus, deadlocks in cooperative transport are also conspicuous. The fact that deadlocks are common and conspicuous makes cooperative transport an ideal task for studying the resolution of deadlocks in collective decisions.

Prior research has revealed aspects of cooperative transport, including selection pressures, ecology, recruitment, and more (reviewed in Berman et al. 2011; Czaczkes and Ratnieks 2013; McCreery and Breed 2014). This previous research has also included detailed descriptions and models of cooperative transport, and in some cases models have been compared with empirical data (Berman et al. 2011; Kumar et al. 2013; Wilson et al. 2014; Gelblum et al. 2015). But these studies have not focused on comparing alternative behavioral rules for overcoming the coordination challenge; thus, our understanding of behavioral rules for deadlock breaking, and for cooperative transport generally, is limited. Some investigators have suggested that ants in groups use the same rules as individual transporters (reviewed in Berman et al. 2011). However, if rules for individual transport were sufficient, one would expect most ant species to be efficient at cooperative transport. This is not the case (Moffett 1992; Czaczkes and Ratnieks 2013), and it is reasonable to think that efficient cooperative transporters have behavioral rules tuned to this task. What behavioral mechanisms separate the coordinated from the uncoordinated transporters?
We use a proof-of-concept model (Servedio et al. 2014) to investigate the behavioral rules, information, and minimum complexity of individuals required in order to break deadlocks. Deadlock breaking has previously been studied in decisions with positive and negative feedback mechanisms (e.g. Pais et al. 2013). Here, we set out to determine if simple individuals employing just one feedback or even no feedbacks can break deadlocks. We model three broad categories of behavioral rules in both deterministic and stochastic contexts. These sets of rules differ in the kinds of information we allow individuals to perceive and the ways this information is used by individuals. We model one spatial dimension, so we examine a decision between two options for direction of travel: left or right. Our goal is not to identify the exact rules employed by all ants, but rather to explore the simplest behaviors and minimum information required to break deadlocks. Thus, we leave the comparison of our predictions with empirical patterns of transport for future research. Like other proof-of-concept models, the value in this work is that it tests the logic of verbal hypotheses and creates predictions that can be empirically tested (Servedio et al. 2014). Our investigations generate hypotheses for cooperative transport adaptations and offer insights into consensus decisions in other groups. The broad modeling approach we employ has been used extensively to elucidate behavior that is difficult to measure in collective systems, including social insects, robots, and beyond (e.g. Couzin et al. 2002; Lerman et al. 2005; Sumpter 2010; Correll and Martinoli 2011; Dornhaus 2012; Pais et al. 2013).

We use this approach to answer two primary questions. First, can realistic, simple behavioral rules reliably overcome deadlocks? As part of this question, we look at what information individuals must minimally receive. Second, what effects do persistence (maximum engagement time with the object) and sensitivity to information have on coordination? In answering these questions we generate hypotheses for cooperative transport adaptations and
provide insight into the factors that affect deadlocks during cooperative transport, and during other collective decisions.

4.3 METHODS

Assumptions

We are interested in the minimum information and complexity requirements for deadlock breaking. We therefore assume individuals have minimal capabilities. As described below, we allow them little information. Our simulated ants also have no memory, in that they do not use information from past experiences to shape future behaviors. Real ants have more capabilities and information than the simulated ants in our models, but to find minimum requirements, we exclude several sources of information that have been demonstrated in one or more ant species. We further simplify real cooperative transport efforts by assuming that all ants are identical.

Ants sense a wide range of stimuli (Hölldobler and Wilson 1990; Åkesson and Wehner 2002; Pielstroem and Roces 2012), though workers of a single species likely can sense only a subset of the total possible information. There are several ways that workers in a cooperative transport group might gain information about what others in the group are doing. They could communicate with one another, but while workers recruit additional help to the object to be carried, often with pheromone trails (McCreery and Breed 2014), there is no evidence of direct communication among ants after the recruitment phase. A simpler possibility is that workers communicate indirectly through the object being carried, an example of stigmergy. This stigmergy mechanism has been hypothesized for ant groups by Kube and Bonabeau (2000) and others (Kube and Bonabeau 2000; Berman et al. 2011; McCreery and Breed 2014). This indirect communication does not require an evolved signal, as workers simply detect physical cues that
necessarily arise when forces are applied to an object. In terms of the kinds of information available in our model, we only consider a narrow set of information that could plausibly be transmitted through the object itself. Specifically, the maximum information we allow individuals to receive about group members’ behavior is the relative sizes of the groups aligned left and right. This information could be transmitted through the object via the magnitude and direction of the object’s movements and/or deformations (Kube and Bonabeau 2000; McCreery and Breed 2014), or there are other possible mechanisms for individuals to estimate relative group sizes, such as direct communication. Our model thus serves as a logical test of the hypothesis that this minimal information is sufficient to break deadlocks. Our assumptions are appropriate based on existing literature regarding complexity requirements for group decisions and hypotheses specific to cooperative transport (McCreery and Breed 2014; Reid et al. 2015a).

**Deterministic Model**

We developed a deterministic, ordinary differential equations (ODE) model that simulates the average behavior of individuals. The model is Markovian – individuals have no memory – but non-linear. We model movement in one spatial dimension implicitly and we use continuous time and continuous abundances of individuals (but see individual-based model below). Individuals are identical, and the total number is fixed at 20; for some analyses we explored the effect of changing group size analytically and by evaluating groups with a total of 6 or 200 individuals. Having a fixed number of individuals is appropriate because the number of workers that can participate in cooperative transport will be limited by the number of grasping points on the object. Furthermore, the behavioral states we model allow varying numbers of individuals to be engaged with the object at any one time. Specifically, our model assumes that
each individual occupies one of three mutually exclusive behavioral states: 1) trying to move the
object to the left, 2) trying to move the object to the right, or 3) disengaged from the object
(Figure 4.1). We do not distinguish between pushing and pulling; individuals pushing from the
left and pulling from the right are both in the “move right” behavioral state. Individuals move
from the disengaged state to an active state by “joining,” and from one of the active states to the
disengaged state by “giving up.” Individuals do not move directly between the two active states,
however, individuals can immediately re-join after giving up. The transition rates are important
model parameters that govern the number of individuals in each behavioral state over time. We
examine these abundances to see the extent to which the group converges on a single direction
under the parameters of a specific model run.

Joining: Disengaged individuals join the transport efforts to the left and right with rate
constants $J_L$ and $J_R$, respectively. The realized joining rates depend on the number of disengaged
individuals: the instantaneous joining rate for the left state is $J_L$ multiplied by the number of
disengaged ants. We assume the joining rate constants do not change in time but may differ from
each other, i.e. individuals may join the “move left” behavioral state at a higher rate than the
“move right” state. If $J_L$ and $J_R$ are not equal, this ensures a directional bias, which is how we
represent individuals having information about the direction of the goal.
Figure 4.1. Model diagram. Individuals belong to one of three behavioral states: moving left, moving right, or disengaged. Individuals move between these states at rate constants $G_L$, $G_R$, $J_L$, and $J_R$.

In real ants, directional cues about the location of the nest come from one or more sources, such as pheromone trails, visual navigation, or path integration (Visscher 2007; Zabzina et al. 2014). Whatever the sensory modality may be, we assume this information is not perfect. That is, even if there is a directional bias, some individuals still choose the other direction (i.e., $J_L, J_R > 0$). Joining rate constants do not vary during the transport effort; for example, we assume groups are not capable of altering their bias in favor of the “winning” direction (here we use the “winning” direction to indicate simply the direction that has more individuals). This makes sense given our conservative assumptions about individuals’ memory and sensory capabilities: individuals that are disengaged, and therefore not in contact with the object to sense information transmitted through it, cannot perceive which direction is winning and have no memory about which direction was winning when they were last engaged.
Giving-up: Individuals in the active behavioral states (left and right) give up at rate constants $G_L$ and $G_R$, respectively. We model three sets of behavioral rules for giving up rates. These sets of rules also differ in the kinds of information individuals act upon (Table 4.1). We do not suggest that all of the variation in cooperative transport behavior in ants is captured by these three sets of rules; rather, we explore these rules to see if such simple rules are sufficient to break deadlocks.

**Table 4.1: Modeled sets of behavioral rules and information required for each.**

<table>
<thead>
<tr>
<th>Rule</th>
<th>Description</th>
<th>Information used</th>
</tr>
</thead>
<tbody>
<tr>
<td>“Uninformed”</td>
<td>If in one of the active states, give up (become disengaged) at a constant rate</td>
<td>None</td>
</tr>
<tr>
<td>“Oblivious”</td>
<td>If in one of the active states, give up more readily when transport is unsuccessful, and less readily when it is “successful” (see text)</td>
<td>Must be capable of measuring the “success” (i.e. extent of coordination) but not the direction of the majority relative to one’s own behavioral state.</td>
</tr>
<tr>
<td>“Informed”</td>
<td>If in one of the active states, and if transport is successful, give up readily if going the opposite way as the majority and less readily if going the same way as the majority.</td>
<td>Must be capable of measuring (i) extent of coordination and (ii) preferred direction of the majority and must compare the latter to one’s own behavioral state.</td>
</tr>
</tbody>
</table>

Behavioral rules differ among different model runs, but within one run of the model all individuals are identical and have the same rules and parameter values. In “uninformed” groups, giving up rate constants, $G_L$ and $G_R$, are equal and do not change over the course of the transport effort. In “oblivious” and “informed” groups (defined in Table 4.1), realized giving up rates change over the course of the transport effort based on the abundances of individuals in the two active behavioral states ($N_R$ and $N_L$). Giving up depends on the “success” of transport. “Success” is operationally defined here as a high extent of coordination, measured as the absolute value of $N_R - N_L$ divided by the total number of individuals in the system. In other words, the extent of
coordination is the degree to which individuals are unevenly distributed across the two active groups.

In oblivious groups individuals can measure success but they cannot detect if they are contributing to or detracting from that success. Individuals give up less frequently when \(|N_L - N_R|\) is high, i.e. when there are many more individuals in one active state than the other, regardless of whether they are currently in the “right” or “left” state. Individuals are oblivious to their own contribution. If the transport is successful because many more individuals are trying to move the object to the left rather than the right, individuals moving right, who are going against the majority, still rarely give up. In ants, this would happen if they were capable of determining when the group sizes are uneven (or a proxy, such as the magnitude of the force on the object), but not in which direction. For example, this might occur if individuals are less likely to give up when they are moving, regardless of the direction.

In informed groups individuals are capable of detecting the same information as in the “oblivious” case, but additionally they can determine if their contribution is with or against the majority. Individuals give up less frequently when there is a higher extent of coordination only if their behavioral state matches the majority. For example, when \(N_L - N_R\) is strongly positive, individuals in the “move left” state give up infrequently while individuals in the “move right” state give up quickly. As discussed above, \(N_L - N_R\) is a measure of success that could be estimated by ants in multiple ways. For example, large values of \(N_L - N_R\) (or highly negative values) will correspond to higher speeds over ground, which an ant might measure by estimating optical flow or her own leg movements.

Equations governing the giving-up rate constants, \(G_L\) or \(G_R\), under each set of rules are listed in Table 4.2 and examples of how these functions behave are illustrated in Figure 4.2. In
addition to the variables $N_R$ and $N_L$, functions for determining $G_L$ and $G_R$ depend on one or more parameters (Table 4.2). These parameters represent persistence and sensitivity, and are discussed below. We chose ranges of parameter values in order to manage computing time while selecting parameter ranges spanning multiple orders of magnitude. Some parameters were also constrained by necessity; for example, the shape parameter $g_1$ must be non-zero.

Table 4.2: Functions governing the giving-up rate constants under each set of rules. Ranges of parameter values explored are in parentheses.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$G_L$</th>
<th>$G_R$</th>
<th>Max $G$ (Persistence$^{-1}$)</th>
<th>Shape parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uninformed</td>
<td>$a$</td>
<td>$a$</td>
<td>$a$ (0.2 – 20)</td>
<td>NA</td>
</tr>
<tr>
<td>(Figure 4.2A)</td>
<td>$g_2$</td>
<td>$g_2$</td>
<td>$g_2$ (0.2 – 20)</td>
<td>$g_1$ (0.1 – 100)</td>
</tr>
<tr>
<td>Oblivious</td>
<td>$\frac{g_2}{g_1 +</td>
<td>N_L - N_R</td>
<td>}$</td>
<td>$\frac{g_2}{g_1 +</td>
</tr>
<tr>
<td>(Figure 4.2B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Informed</td>
<td>$\frac{b_1}{1 + e^{-b_2(N_R - N_L)}}$</td>
<td>$\frac{b_1}{1 + e^{-b_2(N_L - N_R)}}$</td>
<td>$b_1$ (0.2 – 20)</td>
<td>$b_2$ (0.1 – 100)</td>
</tr>
<tr>
<td>(Figure 4.2C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Figure 4.2.** Giving-up rate constants for individuals in the “move right” behavioral state at various levels of success for each set of rules. The x-axis indicates a measure of success: the size difference between the two groups. (A) Uninformed rules, $a = 2$. (B) Oblivious rules, $g_2/g_1 = 2$, $g_1 = 4$ (solid line) or 0.5 (dashed line). (C) Informed rules, $b_1 = 2$, $b_2 = 0.5$ (solid line) or 3 (dashed line). In (B) and (C), dashed lines indicate sharper shape parameters.
Persistence and sensitivity: The giving up rates described above are tunable based on individuals’ persistence and sensitivity to information. These parameters govern the shape and maximum values of the giving-up functions (Figure 4.2). This maximum giving-up rate is the inverse of the engagement time under conditions when individuals give up fastest: when $N_L = N_R$ in the oblivious case and when the difference between $N_L$ and $N_R$ is largest and opposed to the individual’s state in the informed case. We refer to this engagement time as persistence (Czaczkes et al. 2011; McCreery and Breed 2014).

Persistence is individuals’ resistance to changing their behavior based on information (McCreery and Breed 2014), which could come from other individuals in the group, or other sources. Persistence can be measured in actual ants as the time it takes for an individual to give up or change the direction they are trying to move the object being carried. Highly persistent ants keep trying to move the object in the same direction for a long time, even without progress. On the other hand an ant with low persistence will try new strategies frequently, by pulling in different directions or even abandoning the effort temporarily or permanently. Intuitively, one expects a tradeoff for persistence. Groups with high persistence may have long-lasting deadlocks, while groups may also deadlock if no individual is persistent enough. We look at the effect of persistence in our model by varying the maximum possible giving-up rate (Figure 4.2). We ran the model with each of many maximum giving-up rate constants to examine the effect of persistence on extent of coordination; higher maximum giving-up rate constants mean lower persistence and vice versa (Table 4.2).

For the oblivious and informed cases we can also tune the parameters to change the sensitivity of individuals to the success of transport, that is, the magnitude of $|N_L - N_R|$. We do this by changing the shape of the giving-up functions through manipulations of the shape
parameters \((g_1 \text{ and } b_2; \text{ Table 4.2})\), making the transition from low to high giving-up rate constants sharper or more gradual (Figure 4.2). With a gradual shape, when groups are relatively close to deadlocked (near \(N_L = N_R\)), small changes in success lead to only small changes in the frequency of giving-up; individuals with a gradual shape therefore have low sensitivity to transport success. On the other hand, for sharp shapes, a small change in success when \(N_L \approx N_R\) leads to a dramatic change in this frequency; this means individuals are highly sensitive. Differences in sensitivity could be caused by a number of factors, including error in sensing the group sizes. This shape parameter can be quantified for real organisms by fitting functions to data on individuals, for whom cooperative transport efficiencies are experimentally manipulated.

**Differential equations:** The model consists of the following set of differential equations giving the rates of change in the numbers of individuals in each behavioral state (moving left, moving right, or disengaged, respectively):

\[
\frac{dN_L}{dt} = J_L N_D(t) - N_L(t)G_L
\]

\[
\frac{dN_R}{dt} = J_R N_D(t) - N_R(t)G_R
\]

\[
\frac{dN_D}{dt} = N_L(t)G_L + N_R(t)G_R - (J_R + J_L)N_D(t)
\]

where \(N_D\) is the number of individuals in the disengaged state (Fig 1). The ODEs are non-linear due to the dependence of \(G_R\) and \(G_L\) on \(N_R\) and \(N_L\). There is a constant number of total individuals (i.e., \(N_D + N_R + N_L = N = \text{constant}\)), so this is a closed system, making the third differential equation implicit in the first two. Therefore in some cases we present results for the number of ants in the left and right states only. The ODE will always satisfy the following equations at equilibrium, where \(N^*\) is the equilibrium abundance.

\[
\frac{N_L^*}{N_D^*} = \frac{J_L}{g_L(N_L^*, N_R^*)}
\]
\[
\frac{N^*_R}{N^*_D} = \frac{J_R}{G_R(N^*_L, N^*_R)} \tag{5}
\]

\[
\frac{N^*_L}{N^*_R} = \frac{J_L G_R(N^*_L, N^*_R)}{J_R G_L(N^*_L, N^*_R)} \tag{6}
\]

In the uninformed and oblivious cases, \(G_L = G_R\), so equation 6 simplifies to the following.

\[
\frac{N^*_L}{N^*_R} = \frac{J_L}{J_R} \tag{7}
\]

Because \(G_R\) and \(G_L\) are nonlinear functions of \(N_R\) and \(N_L\) in the oblivious and informed cases, it is difficult to solve this system of differential equations analytically. We numerically solved the ODE for each of nearly fifteen thousand sets of parameters, running the model under different sets of behavioral rules, global directional biases, and persistence and sensitivity. The range of parameter space explored for giving-up parameters is shown in Table 4.2. Additionally, we explored directional biases ranging from no bias, to joining rates of 0.01 and 0.9, respectively, for the two directions, a difference of two orders of magnitude; this range in bias provided a comprehensive illustration of the effect of joining bias. We then queried the results for particular metrics of interest, including the maximum extent of coordination on a direction (unevenness in the distribution of individuals across the left and right groups). We obtained numerical solutions using \textit{Mathematica} (version 9.0.1.0) and we analyzed our results using \textit{Mathematica} and R (RStudio version 0.98.977). In addition to the numerical solutions, we analytically explored the stability of deadlocks in the informed case using fixed-point analysis (Strogatz 1994, see Appendix 4-1).

\textit{Stochastic Extension}

Our ODE model makes certain assumptions required for any ODE, including instantaneous updating of information and continuous, rather than discrete, individuals. To test
whether our conclusions are robust to these assumptions, and to look at the potentially important influence of stochasticity, we extended the model to a stochastic framework. The stochastic extension is an individual-based model operating in discrete time. We converted the instantaneous joining and giving-up rate constants \(J_L, J_R, G_L, \text{ and } G_R\) to probabilities of joining or giving up in a given time step with the equation

\[
P_t = 1 - e^{(-R\delta_t)}
\]

where \(P_t\) is the probability of a behavioral shift in one time step, \(\delta_t\) is the length of a time step (here, time steps were always unit length), and \(R\) is the instantaneous rate constant, either \(J_L, J_R, G_L, \text{ or } G_R\). We ran the stochastic simulation for 60 time steps; this duration was more than sufficient to capture transient dynamics. All other model assumptions and parameters were the same as in the deterministic model, including the three sets of rules.

In each time step we allow individuals to change their behavioral state. An active individual changes its status by giving-up with a probability equal to the giving-up probability for that individual’s current state (left or right), and disengaged individuals can change their status by joining. Because disengaged individuals can change their status in one of two ways (joining the left group or the right group), we first calculated the joint probability of an individual joining at all. For individuals that were to join, we then stochastically determined whether they joined left or right using the relative probabilities of each. We ran the stochastic model under the same parameter sets as the deterministic model, querying 1,000 simulations for each set of parameters. As with the deterministic model, we examined the extent of coordination.

We performed and analyzed stochastic simulations in R (RStudio version 0.98.977).
4.4 RESULTS

*Deterministic Model*

Our primary measurement of success is the extent of coordination, which is the difference in the number of individuals in the active behavioral states (left and right) divided by the total number of individuals in the system. If the transport is uncoordinated, there are roughly equal numbers of individuals pulling each direction, and/or most individuals are disengaged.

Streamplot representations of the vector fields portray the dynamical behavior of the system in Figure 4.3. Panels in the figure show different parameter sets, corresponding to each set of behavioral rules with differing directional biases. The streamplots indicate the direction the system tends towards starting from any possible combination of the numbers of individuals in each behavioral state ($N_L$ and $N_R$). The number of disengaged individuals, $N_D$, is not shown explicitly because the total number of individuals is fixed at 20 (i.e., $N_D = 20 - (N_L + N_R)$).
Figure 4.3. Streamplots of system dynamics. These show the direction the system tends towards for various abundances in each behavioral state. A-C: Uninformed rules, $a = 1$; D-F: Oblivious rules, $g_1 = 4$, $g_1/g_2 = 1$; G-I: Informed rules, $b_1 = 1$, $b_2 = 0.5$. A, D, and G: Strong directional bias, $J_L = 0.01$, $J_R = 0.7$; B, E, and H: Weak directional bias, $J_L = 0.3$, $J_R = 0.7$; C, F, and I: No directional bias, $J_L = J_R = 0.3$. 
In the absence of a directional bias ($J_L = J_R$), both the uninformed and oblivious rules have stable equilibria (Figures 4.3C and 4.3F). These are deadlocks, with equal numbers of individuals pulling left and right (as shown in equation 7). Because they are stable, perturbations away from these equilibria lead back to them (Figures 4.3C and 4.3F). In other words, with no directional bias the uninformed and oblivious rules have deadlocks that cannot be broken. In informed groups, however, the equilibrium is unstable even if $J_L = J_R$ (Figure 4.3I). If a deadlock occurs in this case, small perturbations grow exponentially, leading to convergence on one direction, which breaks symmetry. Although an unstable equilibrium occurs across most of the parameter space for informed groups, with small values of the shape parameter $b_2$, the equilibrium is stable and deadlocks are maintained. Thus there is a critical value of $b_2$ at which a phase transition occurs, from stable to unstable equilibrium. Using fixed-point analysis (Strogatz 1994) we analytically determined that this critical value occurs when $b_2$ has the following value:

$$b_2 = \frac{b_1 + 4J}{2JN} \tag{8}$$

where $J$ is the joining rate constant for each side ($J = J_L = J_R$) and $N$ is the total number of individuals in the system. This indicates that total group size affects deadlock breaking. Smaller groups require higher sensitivity ($b_2$) to break deadlocks even in the informed case, and sensitivity is less important for large groups. Details of the fixed-point analysis are included in Appendix 4-1.

When a directional bias is present ($J_L \neq J_R$) more individuals attempt to move the object in the direction favored by the bias, regardless of the set of rules (Figure 4.3, two left-most columns, also see equations 6 and 7). This is true regardless of the initial conditions for uninformed and oblivious groups; for informed groups, a large enough difference in the initial group sizes can overcome a joining bias (see rightmost portion of Figures 4.3G and 4.3H). The
presence of a directional bias increases the extent of coordination, and, intuitively, strong biases lead to more coordination than weak ones (Figure 4.3 left column compared with middle column). However, for a given directional bias, individuals in informed groups are still more coordinated than individuals in uninformed or oblivious groups. Stable equilibria involving individuals working against one another still occur with a weak bias using these sets of rules (Figures 4.3B and 4.3E). With a sufficiently strong directional bias, in both uninformed and oblivious groups, the system moves to a state with almost no individuals going against the bias (Figures 4.3A and 4.3D), but there are still a substantial number of disengaged individuals who do not contribute to the effort (shown implicitly in Figure 4.3). This is because the disengaged group is constantly replenished by individuals giving up from the two active states. There are almost no disengaged individuals in informed groups. Thus, a directional bias allows for an unequal distribution of individuals between the two active states regardless of the behavioral rules, but the informed case still outperforms the other behavioral rules in that it maximizes engagement and the difference in group sizes.

**Stochastic Model**

The stochastic results are very similar to results from the deterministic model. Figure 4.4 shows the number of individuals in each behavioral state for two examples of stochastic simulations, under the same parameter sets shown in Figure 4.3. Figure 4.4 also includes the deterministic results. Deterministic and stochastic results match closely for each set of parameters except the informed case with no directional bias. This highlights the importance of stochasticity in this case. Without stochastic perturbations away from equilibrium groups remain deadlocked. In the stochastic model, perturbations are amplified, breaking symmetry and leading
to consensus. Histograms of the behavior of the stochastic model across 1,000 simulations, at specific times, as well as deterministic results at those times, are shown in Figure 4.5.

**Figure 4.4.** Abundance of ants in each behavioral state over time. Includes two example simulations with each set of parameters. Blue: number moving right, Red: number moving left, Black: number disengaged. Dashed lines show deterministic model behavior. Columns are different directional biases and rows are different sets of behavioral rules. The parameter values are the same as in the analogous panels in Figure 4.3. Uninformed rules: $a = 1$; oblivious rules: $g_1 = 4, g_1/g_2 = 1$; informed rules: $b_1 = 1, b_2 = 0.5$. Strong directional bias: $J_L = 0.01, J_R = 0.7$; weak directional bias: $J_L = 0.3, J_R = 0.7$; no directional bias: $J_L = J_R = 0.3$. 
Figure 4.5. Histograms showing the state of 1,000 simulations at given time points. The x-axis shows the number of ants, and the y-axis shows the number of simulations for which the given behavioral state had that many ants at that time. Blue bars are for ants moving right, red bars are for ants moving left, and black bars are for disengaged ants. Bars appear purple when red and blue overlap. Dashed lines show the abundance of each behavioral state in the deterministic model. The parameter values are the same as in the analogous panels in Figures 4.3 and 4.4. Uninformed rules: $a = 1$; oblivious rules: $g_1 = 4, g_1/g_2 = 1$; informed rules: $b_1 = 1, b_2 = 0.5$. Strong directional bias: $J_L = 0.01, J_R = 0.7$; no directional bias: $J_L = J_R = 0.3$.

In all other respects, deterministic and stochastic results were very similar despite differences in the formulations of these models. When a directional bias is present more individuals try to move the object in that direction than in the other direction under our initial conditions of all individuals beginning as disengaged. In the absence of a directional bias, roughly equal numbers of individuals are in each active state in uninformed and oblivious groups, while individuals converge on either direction in informed groups. In each of 1,000 simulations, the informed case allowed for convergence to a pure state (every individual or nearly every individual in the system transporting in the same direction) even with no directional
bias (Figure 4.5). On the other hand, oblivious groups perform no better than uninformed groups, and neither of these sets of rules ever allowed for convergence on one direction.

When a directional bias is present, the informed case still leads to strikingly different performance than either of the other sets of rules. Individuals converge rapidly in informed groups, while in oblivious or uninformed groups, convergence, which we define as an increasing coordination through time until all individuals are pulling the same direction, does not occur. There are more individuals pulling in the direction of bias but coordination does not increase over time (Figures 4.4 and 4.5).

**Effect of persistence and sensitivity**

Figure 4.6 shows the effect of persistence – or maximum engagement time – on the extent of coordination in the deterministic model for groups with total size fixed at 20 (see Appendix 4-2 for results for other group sizes). The extent of coordination reported is the maximum observed over the time period evaluated. Parameter sets that converge more quickly on a direction will have a higher extent of coordination in that time period, and shorter deadlocks. Results in Figure 4.6 are therefore comparable across parameter sets, with higher agreement indicating more efficient transport. Because small perturbations away from equilibrium do not occur in the deterministic model, Figure 4.6 shows no coordination without directional bias.
**Figure 4.6.** Effect of persistence (maximum engagement time, i.e. the inverse of the maximum giving-up rate constant) on maximum coordination. Maximum giving-up rate constant is the maximum possible as defined by the function (Table 4.2), actual values will depend on the number of individuals in each group. Extent of coordination is defined as the difference in the number of individuals pulling right and left, divided by the total number in the system. Maximum coordination is the maximum observed over a given time period; higher values on the y-axis indicate faster convergence. (A) uninformed rules, (B) oblivious rules, (C) informed rules. Lines with smaller dashes indicate larger directional bias, and the solid line indicates no bias (there is no coordination without a directional bias in the deterministic case). Red and blue lines indicate “sharp” and “gradual” shapes (sensitivities), respectively. Parameter values for shape match those in Figure 4.2.

The effect of persistence depends on the behavioral rules (Figure 4.6). In uninformed and oblivious groups, being highly persistent – having a low maximum giving-up rate constant – increases coordination (Figures 4.6A and 4.6B). In informed groups there is an optimal persistence value that maximizes coordination. The extent to which persistence affects coordination is stronger for small directional biases; at high directional biases there is a wide range of persistence values that result in high coordination. These results were not qualitatively different for different total group sizes, except that sensitivity, or sharpness of the giving-up function, was more and less important for smaller and larger groups, respectively (Appendix 4-2).

For oblivious and informed groups, the sensitivity changes the effect of persistence (Figures 4.6C and 4.7); the uninformed case has no sensitivity parameter. In the oblivious case,
sharper functions (lower values of $g_1$) increase coordination for a given persistence value. In the informed case there is a critical sensitivity below which deadlocks cannot be broken, as discussed above and in Appendix 4-1. This threshold depends on group size. Above this threshold, sharper functions (higher values of $b_2$) further increase coordination, which has the effect of widening the range of persistence values that lead to coordination. For a moderate group size of 20 individuals, with a gradual shape and a small directional bias, there is a narrow range of persistence values that allow for high coordination. At small group sizes only groups with higher sensitivity or relatively strong directional bias coordinate successfully regardless of persistence, while large groups successfully coordinate across a wide range of persistence values regardless of sensitivity and bias (Appendix 4-2). Figure 4.7 shows in detail the extent of coordination for moderately sized groups with a wide range of directional biases and persistence values for two shape values, both relatively gradual (see Appendix 4-3 for small and large groups).
**Figure 4.7.** Effect of persistence (inverse of maximum giving-up rate constant) on maximum coordination in informed groups at low (gradual) shape values. Maximum giving-up rate constant is the maximum possible as defined by the function, actual values will depend on the number of individuals in each group. Extent of coordination is defined as the difference in the number of individuals pulling right and left, divided by the total number in the system. Maximum coordination is the maximum observed over a given time period, rather than an absolute maximum; higher values on the y-axis indicate faster convergence. Left column: shape parameter, $b_2 = 0.5$, which corresponds to the solid line in Figure. 4.2C. Right column: $b_2 = 1$, which is less gradual.

### 4.4 DISCUSSION

Can relatively simple individuals with minimal information break deadlocks? Our results show that, indeed, individuals with simple behavioral rules and no memory can break deadlocks. However, only individuals in our informed case convincingly succeeded. These individuals followed simple rules: 1) give up more readily if one is moving against the majority and 2) do this to a greater extent for extreme majorities than slight majorities. Using these simple rules, with minimal information available, groups rapidly converge on a single travel direction, even when this required symmetry-breaking. Our deterministic and stochastic models agree, despite being formulated differently and having contrasting assumptions about individuals and time. This suggests that our conclusions are robust to specifics of model formulation.
In terms of information, it is sufficient for coordination for individuals to only be capable of measuring the direction that the majority of the group is trying to move the object and the relative sizes of the groups moving each direction (or a proxy). This information is crucial; with insufficient sensitivity to these group sizes (low \( b_2 \)) groups do not form a consensus. While sensitivity must be sufficient, it does not need to be high. As further discussed below, groups with only modest sensitivity were still coordinated across a wide range of other parameters. Thus, various proxies for relative group sizes may be accurate enough to break deadlocks. For example, individual ants could gain this information through stigmergy on the object being carried. If this is the case, a single sensory mode may provide all necessary information in informed groups. In nature, ants may have other information available, or may use different behavioral rules, but we show that by using these simple rules, groups are successful.

If individuals have global directional cues that correspond to a shared directional bias, this helps promote coordination regardless of the other information available. Additionally, if there is only one correct direction, for instance if there is a single nest entrance, a shared bias towards the nest would help ensure the group converges on the appropriate direction. But directional bias is neither necessary, nor sufficient, for convergence on a decision.

This makes sense considering the high variation in cooperative transport ability among ant species. We expect workers of all species to be good at knowing the direction of the nest. So we expect directional biases to be common among species, at least for situations with only one correct direction. Considering that efficient cooperative transport is comparatively rare among ants (Moffett 1992; Czaczkes and Ratnieks 2013), the presence or absence of directional bias is not a good explanation for the observed variation in efficiency. On the other hand, the behavioral rule of giving up more readily when an individual is moving against the majority is a potential
adaptation that dramatically improves efficiency. Future research should test whether efficient transporters have this adaptation.

We also investigated the effects that persistence and sensitivity (the sharpness of the giving-up function) have on coordination. These effects are complex and depend on the total group size and the behavioral rules. In the uninformed and oblivious cases, groups are most coordinated if individuals are highly persistent. While somewhat surprising, this makes sense in light of a tradeoff in persistence. Groups of highly persistent individuals may pull in opposing directions for a long time, but if movement does occur, either because of a directional bias or due to random fluctuations, the progress continues; they are unlikely to change their direction.

This suggests that high persistence allows species without other adaptations for cooperative transport, for instance those with behavioral rules similar to our uninformed or oblivious rules, to at least sometimes succeed at bringing a large object home to the nest. In such species, individuals are equally likely to give up whether they are helping or hurting the effort; even when successful movement occurs, individuals pulling with the motion may give up. High persistence makes it less likely that anyone will give up, allowing existing movement to continue. If, as in our model, individuals are identical, the individuals going the wrong way will also be unlikely to give up, so to minimize the length of deadlocks there should only be a small number of these individuals. A sufficient directional bias would accomplish this, and directional biases should be common in many circumstances (such as if the object is relatively far from the nest). So if high persistence is paired with a directional bias, it may allow ant species with rudimentary behavioral rules to conduct cooperative transport. Analogously, agents involved in any decision between two options, when they are unable to determine which option is winning, should be persistent to maximize the chance that a single option will be chosen.
In contrast to these results, in the informed case there is an optimum persistence value; groups with individuals more or less persistent than this value will be less coordinated. But the importance of persistence depends on directional bias, on the sharpness of the giving-up function, and on the total group size. In most of the parameter space of our model, the range of persistence values that lead to high coordination is wide. Only when the directional bias is low and the sensitivity is above the critical threshold but still gradual does one find a narrow peak in coordination around the optimum persistence. This was especially true for smaller group sizes. Large groups had a wide range of persistence values that would lead to coordination regardless of sensitivity, indicating that it may be easier to coordinate in a large group rather than a small group. This makes sense given that small groups will be more affected by the behavior of single individuals. In order for informed individuals in groups of small to moderate size to be highly coordinated, they must have one, but do not need more than one, of the following: high directional bias, high sensitivity to the sizes of the two groups, or finely-tuned persistence. Each of these is a potential adaptation for efficient cooperative transport in informed groups. This flexibility makes the behavioral rules in the informed case relatively robust to deficiencies in the individuals’ capabilities as long as they have at least minimal accuracy in sensing group sizes.

Because we did not constrain our model by tuning it to a particular species, our results are applicable to other collective decisions. A system in which groups must decide among multiple options is vulnerable to deadlocks, especially when the options are relatively equal (analogous to having no directional bias); small group size may also make deadlocks more likely. One of the best studied examples of collective decisions is nest-site selection in social insects (reviewed in Visscher 2007). As discussed above, some recent work on the “stop-signal”
in honeybees focuses on how this signal prevents deadlocks in nest-site selection (Niven 2012; Seeley et al. 2012b; Pais et al. 2013).

The outcome of our deterministic model with respect to the effect of behavioral rules looks similar to the results of Seeley et al. (2012) and Pais et al. (2013), who each investigated decision-making dynamics in honeybee nest site selection with similar models. For example, compare Figure 4.3 here to Figure 3C in Seeley et al. (2012) and the inset in Figure 2 in Pais et al. (2013). Both models investigate the accumulation of “votes” for one of two, mutually exclusive choices in a decision, and in each case the number of individuals aligned with the two options determines which option is chosen. A key difference between the models, however, involves the timing of the decision. In honeybee nest-site selection, a decision is reached when a quorum of scouts is present at one of the potential nests (Seeley 2010). In cooperative transport, an initial decision is reached when the difference between the number of individuals in each group reaches a certain threshold – enough to begin movement – rather than when the absolute number of individuals in a particular group is high. Perhaps a more important difference between these models relates to communication. Unlike our model the Seeley et al. (2012) and Pais et al. (2013) models include direct communication among individuals. Honeybee scouts actively advertise for a particular nest site (a positive feedback mechanism) and stop other scouts from advertising for a different site using the stop signal (a negative feedback mechanism) (Dornhaus 2012). Our model produces similar dynamics using a simpler mechanism. In informed groups, positive and negative feedbacks are combined into a single mechanism that requires no signals. An individual is less likely to give up if her faction is large compared to the other faction (positive feedback), and more likely to give up if the opposite is true (negative feedback,
analogous to cross-inhibition). Informed individuals only need to measure the relative group sizes to make effective decisions.

The Seeley et al. (2012) and Pais et al. (2013) models elegantly and realistically reproduce the dynamics of nest-site selection in honeybees. Our model is simpler, yet produces similar dynamics in terms of the accumulation of votes for a single option, indicating that direct communication among individuals is not necessary for a decision in the case of cooperative transport. The fact that some of our results are similar lends credence to the idea that results from one collective decision-making system can be generalizable to others. Among collective systems, social insects are uncommonly apt for experiment, since individuals are easily observed and manipulated. Because lessons are transferable across at least some systems, we can use social insects as model systems for other systems that are harder to study, such as neuronal networks.

Our model demonstrates that simple behavioral rules can lead to a consensus about travel direction during cooperative transport, even without a directional bias. Our simulated ants had no memory, limited sensory ability, and followed only simple rules, yet made decisions rapidly in informed groups. We identify a potential adaptation – giving up more readily when going against the majority – that allows for deadlock-breaking, and may explain why we see such large variation in cooperative transport ability among ant species. While it is currently not possible to directly measure this adaptation in ants, the consequences we have modeled here can, and should, be measured to see if real ants use this behavioral rule. Our model reproduces dynamics similar to those of other decision-making processes (Seeley et al. 2012b; Pais et al. 2013), and our conclusions are generalizable to other collective decisions. Though cooperative transport is a challenging task that requires coordination, behavioral complexity is not a prerequisite for success.
CHAPTER 5

Individual persistence promotes group coordination during cooperative transport in ants

5.1 ABSTRACT

When groups of ants work together to carry large objects – i.e. engage in cooperative transport – they must form consensus on a single travel direction. In many species, groups deadlock because they are unsuccessful at this decision. In other collective decisions, such as nest site selection in honeybees, individuals’ enthusiasm, or recruitment intensity, for a given option is an important parameter that affects the group’s ability to select among multiple alternatives. A similar mechanism may be important during cooperative transport in ants, and may account for differences among species in their ability to coordinate. Results from theoretical models suggest that individuals’ persistence – their reluctance to give up or change their preferred direction – may promote coordination within groups. Groups in which individuals were more persistent were more successful in a theoretical context. As an empirical test of this hypothesis, I examined cooperative transport in four species of ant that differ substantially in their group-level coordination, from exceedingly coordinated in carrying objects to rarely successful. I measured two types of persistence at the individual level – engagement time and directional fidelity – and I measured group coordination for each species. In one species, *Formica podzolica*, I also manipulated persistence by adding one or more artificial, infinitely persistent ants to existing cooperative transport groups. Species in which individuals were more persistent formed more coordinated transport groups and adding two infinitely persistent ants to existing groups moderately increased their coordination. These results support the hypothesis that high individual

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3 This paper is currently in review at *Insectes Sociaux*.
persistence promotes group coordination during cooperative transport, and this study informs the mechanisms of emergent coordination.

5.2 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, 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. 2012b). During these decisions, workers advertise for particular nest options until a quorum is reached. Importantly, individuals advertise sooner and/or more
intensely for higher quality options (Mallon et al. 2001; Visscher 2007), and may attempt to prevent other workers from advertising for different options (Niven 2012; Seeley et al. 2012b; Pais et al. 2013). Thus, individuals’ enthusiasm for their favored option affects the ability of colonies to choose 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 the object in the same direction if transport is unsuccessful (McCreery and Breed 2014). 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 that 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. Persistence has not previously been evaluated for initial collective decisions about travel direction during cooperative transport. McCreery et al. (2016a) defined persistence as individuals’ resistance to giving up or to changing the direction they are trying to move the object. This combines two behaviors – giving up and changing direction – that may be useful to examine separately. I define two types of persistence: engagement time – how long individuals spend attempting to move an object regardless of direction – and directional fidelity – how long individuals spend trying to move in a particular direction before changing.

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. A logical measure of coordination is efficiency, but group efficiency has not been quantified for the vast majority of ant species (but see e.g. Moffett 1988; Traniello and Beshers 1991; Franks et al. 1999; Buffin and Pratt 2016). When efficiency has been assessed, researchers have not used a standard measure, making comparisons of transport effectiveness among species difficult or impossible. Furthermore, researchers have often used measures that are valuable for examining ecological and evolutionary implications of cooperative transport, but that do not provide direct information about coordination. Here, I measured coordination using sinuosity, which is the ratio of the total path length of the group to
the displacement. As described further in the methods section, sinuosity is a more direct measure of coordination than previously used efficiency measures, and is well suited for use in comparing coordination across species.

I evaluate how persistence – i.e. engagement time and directional fidelity – affect cooperative transport coordination. Based on theoretical results, I hypothesize that high persistence increases coordination (McCreery et al. 2016a). By measuring individual behavioral traits and their effect on group coordination, I aim to directly explore the mechanisms of emergent behavior. I focused on the following three questions. 1) How do engagement time and directional fidelity differ among species? 2) Are species with higher engagement time and directional fidelity more coordinated? 3) Does changing the behavioral makeup of groups affect coordination? I conducted two experiments. In experiment 1, I measured engagement time, directional fidelity, and coordination in four species to explore questions 1 and 2. In experiment 2, I changed the behavioral makeup of cooperative transport groups in one species to alter engagement time and directional fidelity, observing how these changes affected coordination.

5.3 METHODS

Study System

In experiment 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). Experiment 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. 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 experiment are included in Table 5.1.
Table 5.1 Data structure information and mean worker mass and bait mass for each species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean worker mass</th>
<th>Sample size (# of colonies)</th>
<th>Sinuosity sample size (# of colonies)</th>
<th># of attempts recorded</th>
<th>Mean bait mass (range)</th>
<th>Sample size (# of colonies)</th>
<th>Mean (range)</th>
<th>Control</th>
<th>One artificial ant</th>
<th>Two artificial ants</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. longicornis</em></td>
<td>0.43 mg</td>
<td>45 (5)</td>
<td>14 (4)</td>
<td>39</td>
<td>0.11 g (0.080 – 0.18)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>F. podzolica</em></td>
<td>3.4 mg</td>
<td>41 (2)</td>
<td>15 (6)</td>
<td>47</td>
<td>0.90 g (0.57 – 1.15)</td>
<td>47 (10)</td>
<td>1.05 g (0.86 – 1.18)</td>
<td>45 (10)</td>
<td>42 (10)</td>
<td>16 (6)</td>
</tr>
<tr>
<td><em>F. obscuripes</em></td>
<td>5.2 mg</td>
<td>42 (4)</td>
<td>11 (2)</td>
<td>25</td>
<td>1.24 g (0.95 – 2.03)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>F. pallidefulva</em></td>
<td>2.8 mg</td>
<td>33 (1)</td>
<td>9 (1)</td>
<td>30</td>
<td>1.47 g (1.00 – 1.86)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Experiment 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 consensus has been reached; therefore it is valuable to measure persistence when the group is unsuccessful. I measured two types of persistence, engagement time and directional fidelity, as well as coordination, in the four study species, to see how individual persistence affects the ability of groups to choose a travel direction.

To characterize how the individual traits engagement time and directional fidelity 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 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.
Engagement time and directional fidelity: To measure engagement time and directional fidelity of individuals I pinned dead house crickets (*Acheta domestica*) to the trial surface (paper or foam) and video recorded ants’ attempts to transport them. 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 left the cricket, or when the worker changed the direction of attempted movement. My measure of engagement time was the workers total time spent pulling divided by the amount of time that individual was recorded. My measure of directional fidelity was the average length of time the individual tried to move the cricket in a given direction before changing direction or giving up. 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 5.1.

Coordination: As discussed above, cooperative transport efficiency has not been quantified for the majority of ant species, and when it has, there has not been a standard measure of efficiency. Researchers have often measured the rate of food delivery to the nest, or related measures such as speed (Moffett 1988; Traniello and Beshers 1991; Franks et al. 1999; Buffin and Pratt 2016). While this is valuable for examining the ecological and evolutionary context of cooperative transport, it is less informative about the extent and mechanisms of coordination in a group. Other factors unrelated to coordination, such as colony size, foraging effort, and food availability also affect the rate of food delivery. Furthermore, poorly coordinated groups may occasionally succeed at bringing a large object to their nest, or groups that are highly coordinated may fail to do so, perhaps because they have poor information about nest direction. To isolate
coordination from other factors affecting nest delivery, I used 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. Sinuosity is also particularly well suited for use in comparing coordination across species, as this measure is not affected by other species-specific traits such as walking speed or worker strength.

I measured the sinuosity of groups by placing large baits on paper or foam boards next to colonies and video recording cooperative transport attempts. 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, because it cannot be measured for transport failures with no movement. Therefore, as an additional measure of coordination, I observed the proportion of transport attempts in which groups moved at least 10 cm. I considered groups moving 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 were not counted as attempts. 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 5.1. I obtained mean mass estimates to confirm that our bait masses were
reasonable (Table 5.1). 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. In order 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 baits for persistence measurements, baits used for coordination were reused for multiple trials within a colony, but not across colonies. Sample sizes for all measurements are included in Table 5.1. I measured sinuosity for a subset of successful attempts recorded. For *F. podzolica*, I measured sinuosity from some control trials from Experiment 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 does 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.
Experiment 2: Persistence Manipulation

To explore whether altering persistence affects coordination (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. Their addition increased both the mean and the variation in the transport group of both types of persistence: engagement time and directional fidelity. For each trial I measured the sinuosity of the transport effort both before and after adding artificial ants to see the change in sinuosity.

*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 (Figure 5.1A). I did not need to attach bait to the chain, as *F. podzolica* workers naturally, consistently, and enthusiastically pulled on the plain metal chain. 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 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.
**Figure 5.1:** 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 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 treatment simulating one artificial ant – twice this weight was added to simulate two ants.

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 calculated 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. I used the coefficient of friction and the weight of chain each worker successfully moved to calculate the force that 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 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%.

*Experiment 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 (Figure 5.1B). 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 transported. I protected my apparatus from wind to keep the force on the bait constant. The direction of the added force was different from the overall direction of movement, and 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. I extracted bait trajectory data from the videos manually, as described above for sinuosity measurements for Experiment 1.

**Statistical Analyses**

All statistical analyses were performed in R, version 3.2.2 (R Core Team 2015).

*Question 1: How do engagement time and directional fidelity differ among species?* I compared the individual-level traits engagement time and directional fidelity among species using analysis of variance (ANOVA), on log-transformed data. For both engagement time and directional fidelity, log-transformed data fit the assumption of normality. I used Tukey’s post-hoc comparisons to compare species pairs. To see whether engagement time and directional fidelity 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 engagement time and directional fidelity more coordinated?** I first characterized how species differed in coordination. I used a Pearson’s $\chi^2$ 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 engagement time and directional fidelity 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, I could not measure persistence of members of specific groups for which I had efficiency data. 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 engagement time or directional fidelity with either sinuosity or proportion of attempts that succeeded; 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 coordination?** 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.

5.4 RESULTS

1) How do engagement time and directional fidelity differ among species?

*P. longicornis* workers had the highest engagement time and directional fidelity (Figure 5.2, Table 5.2). *F. podzolica* and *F. obscuripes* both had moderate values, with *F. podzolica* having slightly higher mean directional fidelity and slightly lower mean engagement time than *F. obscuripes*. *F. pallidefulva* workers had the lowest measurements for both traits. There were significant differences among species both for engagement time (F = 43.18, p < 0.0001), and directional fidelity (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 directional fidelity, and *F. pallidefulva* and *F. obscuripes* only marginally differed in engagement time (p = 0.051). Complete results of post-hoc comparisons are included in Appendix 5-1. Qualitatively, I found that *P. longicornis* workers had the largest variation in persistence measures in addition to being the most persistent (Figures 5.2 and 5.3). This was true for both engagement time and directional fidelity, and one *P. longicornis* attempted to pull a pinned cricket consistently in the same direction for more than 90 seconds, 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.
Figure 5.2: Individual measures of persistence. Letters indicate significant differences, from Tukey’s post-hoc comparisons. Left panel: Engagement time for each species, measured on individuals (species significantly differ: F = 43.18, p < 0.0001). Engagement time is the proportion of time an individual was in the video frame that the individual was actively trying to move the cricket. Right panel: Directional fidelity 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 directional fidelity was > 90 seconds. 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 5.2: Engagement time and directional fidelity for each species. Sample sizes for these persistence measurements are included in Table 5.1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean engagement time, proportion of time pulling (s.e.)</th>
<th>Mean directional fidelity, seconds (s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. longicornis</td>
<td>0.360 (0.0050)</td>
<td>8.63 (0.29)</td>
</tr>
<tr>
<td>F. podzolica</td>
<td>0.136 (0.0018)</td>
<td>3.62 (0.068)</td>
</tr>
<tr>
<td>F. obscuripes</td>
<td>0.093 (0.0017)</td>
<td>4.61 (0.072)</td>
</tr>
<tr>
<td>F. pallidefulva</td>
<td>0.0567 (0.0014)</td>
<td>2.35 (0.074)</td>
</tr>
</tbody>
</table>
Figure 5.3: Directional fidelity (mean time moving a particular direction before changing) and engagement time (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 directional fidelity was > 90 seconds.

Engagement time and directional fidelity were correlated; individuals with high engagement time tended to have high directional fidelity (Pearson’s $r = 0.69$, $p < 0.0001$, Figure 5.3). This correlation was significant within each species as well as for the pooled data ($P. longicornis$: $r = 0.68$, $p < 0.0001$; $F. podzolica$: $r = 0.65$, $p < 0.0001$; $F. obscuripes$: $r = 0.54$, $p = 0.0002$; $F. pallidefulva$: $r = 0.56$, $p = 0.0007$).

2) Are species with higher engagement time and directional fidelity more coordinated?

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 5.3, Figure 5.4). 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. 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 Figure 5.4 and Appendix 5-1. *P. longicornis* had significantly lower sinuosity than all other species, and *F. obscuripes* groups had marginally lower sinuosity than groups of *F. pallidefulva* ($p = 0.059$).

**Table 5.3:** Coordination in each species.

<table>
<thead>
<tr>
<th></th>
<th>Attempts</th>
<th>Successes</th>
<th>Proportion successful</th>
<th>Mean sinuosity (s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. longicornis</em></td>
<td>39</td>
<td>38</td>
<td>97.4%</td>
<td>1.24 (0.017)</td>
</tr>
<tr>
<td><em>F. podzolica</em></td>
<td>47</td>
<td>45</td>
<td>95.7%</td>
<td>2.14 (0.057)</td>
</tr>
<tr>
<td><em>F. obscuripes</em></td>
<td>25</td>
<td>22</td>
<td>88.0%</td>
<td>1.94 (0.073)</td>
</tr>
<tr>
<td><em>F. pallidefulva</em></td>
<td>30</td>
<td>8</td>
<td>26.7%</td>
<td>4.33 (0.24)</td>
</tr>
</tbody>
</table>
Figure 5.4: 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 X-squared = 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.

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 engagement time and success was marginal, species with higher engagement time tended to be more likely to succeed (Kendall’s tau = 1, p = 0.0833). This p value is the lowest possible for a two-tailed Kendall’s rank correlation with four points. Likewise, the correlation between directional fidelity and sinuosity was marginal, species with higher directional fidelity 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 (directional fidelity with success: Kendall’s tau = -0.67, p = 0.33; engagement
time 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.

3) Does changing the behavioral makeup of groups affect coordination?

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 experiment 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 Figure 5.1B.

Sinuosity measurements before and after the addition of artificial ants are shown in Figure 5.5 (white boxes: before addition, gray boxes: after addition). Control trials, with no artificial ants added, did not result in changed sinuosity, 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 engagement time and directional fidelity 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 engagement time and/or directional fidelity and transport efficiency.
Figure 5.5: 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.

5.5 DISCUSSION

Ant species differ substantially in their ability to cooperatively transport large objects. This variation likely arises from differences in ecology and evolutionary history. For example, species in areas with 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). The ecological and evolutionary background of ant species may explain, in part, why cooperative transport may be more
important for some species than others, and why species’ abilities differ. 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 (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 found that ant species differ substantially in both measures of persistence: engagement time and directional fidelity (question 1). *P. longicornis* workers had a mean engagement time more than six times that of *F. pallidefulva*, and a mean directional fidelity nearly four times as high. *P. longicornis* workers were also by far the most coordinated of these four species. Since the patterns of engagement time and directional fidelity across the four species were similar, I could not isolate the potential effects of these traits individually when evaluating questions 2 and 3. 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. Intuitively, 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. My observations support this, as *P. longicornis* workers also had, qualitatively, the highest variation in both engagement time and directional fidelity. 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, engagement time and directional fidelity, were correlated – species with high engagement time also had high directional fidelity – 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 engagement time), but were unlikely to change the direction they tried to move it (moderately higher directional fidelity) (Figure 5.2). The differences were not large enough for me to disentangle the effects of these traits with confidence, but the coordination results for these species suggest new hypotheses about the effects of high engagement time and high directional fidelity separately. High engagement time may be more important for getting moving at all, while high directional fidelity may be more important for low sinuosity. *F. obscuripes* workers were less likely to succeed at moving a large item than *F. podzolica* workers, but when they did succeed, they tended to have lower sinuosity. *F. pallidefulva* workers, on the other hand, have both low engagement time and low directional fidelity. These groups rarely succeed, and often have strikingly high sinuosity when they do.

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 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 Experiment 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 I measured were correlated; individuals with high engagement time tended to also have high directional fidelity. As these traits also seemed to promote coordination, individuals with high engagement time and directional fidelity 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 quality of nest location information.

While my study focused on persistence, the species 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 engagement time and directional fidelity. Among the species 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.
6.1 ABSTRACT

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

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4 This paper was published in *Journal of Experimental Biology* with Zachary A. Dix, Michael D. Breed, and Radhika Nagpal
6.2 INTRODUCTION

From multi-cellular organization to massive animal migrations, emergent group behaviors are ubiquitous and drive much of the complexity of the biological world. Tasks are often accomplished without a leader (Camazine et al. 2001), as impressive group behavior emerges from individual-level interactions. Ant colonies are model systems for studying emergent group behavior due to the complexity and scale of the tasks they cooperatively accomplish. A crucial task for many animal groups, including ants, is making collective decisions, and a substantial body of studies deal with how groups accomplish this with discrete, single-step decisions (Deneubourg and Goss 1989; Conradt and Roper 2005; Sumpter and Pratt 2009), such as nest site selection in honey bees or *Temnothorax* ants (Pratt et al. 2002; Pratt 2005; Seeley 2010). In contrast, we know less about how groups collectively accomplish complex tasks that require a series of decisions, each building on previous ones. This type of behavior is akin to problem solving, and has been studied primarily in individuals rather than groups. For example, maze-solving has been studied in many taxa including rats (Mulder et al. 2004; Yoder et al. 2011), and single-celled slime molds (Nakagaki et al. 2000; Reid et al. 2012; Reid and Beekman 2013). Groups making serial decisions face the additional challenge of maintaining consensus – defined as agreeing on a single option (Sumpter and Pratt 2009). In this study we examined collective problem solving by coordinated groups of ants in a task similar to a maze.

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

How a group solves this problem – their strategy – impacts the kinds of obstacles they can successfully navigate. Consider a simple strategy: when a transport group encounters an obstacle, they choose a direction to move around obstacle perimeter until they can again move, unobstructed, toward the nest. This strategy requires information about nest direction and the ability to form consensus on travel direction, both of which are plausible for groups of ants. However, this simple strategy only works with simple obstacles; groups using this strategy would get stuck in a concave obstacle, which would require moving away from the nest to succeed. On the other hand, navigation strategies exist that would be successful for any possible obstacle, but require more information (e.g. Table 6.1; Kamon and Rivlin 1997; Murphy 2000). We define these strategies as “robust” because they are successful over a range of obstacle shapes. But robustness comes at a cost in terms of energy and information processing. Thus, there is a trade-off between simple strategies that are easy for groups to execute but may fail, and strategies that are robust with respect to obstacle shapes, but more costly.
Table 6.1: Predictions for efficiency of navigation in the wall and the cul-de-sac with example strategies of different robustness.

<table>
<thead>
<tr>
<th>Example Strategy</th>
<th>Description</th>
<th>Prediction</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>Groups move in the direction of the nest, however when that direction is obstructed they are unable to form consensus on a new direction.</td>
<td>Groups fail to navigate any of the obstacles.</td>
</tr>
<tr>
<td>Simple 1</td>
<td>Groups move in the direction of the nest whenever possible. If obstructed, the group can form consensus on a new direction, and they follow the obstacle perimeter until the nest direction is available. This requires the ability to estimate nest direction and to form consensus on a travel direction even when the nest direction is unavailable.</td>
<td>Groups succeed at navigating the wall but fail to navigate the cul-de-sac, because in the cul-de-sac the nest direction becomes available before navigation is complete. This strategy fails on all non-convex obstacles (Lumelsky and Stepanov 1987).</td>
</tr>
<tr>
<td>Extremely robust 1</td>
<td>Groups move towards nest direction whenever possible; if obstructed, groups move around obstacle as in the Simple 1. However, the group only leaves the obstacle perimeter when the nest direction is available and the nest is closer than at any other point during navigation. This strategy requires the ability to estimate distance to the nest.</td>
<td>Groups will successfully navigate both the wall and the cul-de-sac with maximum efficiency (sinuosity = 1 for each). This strategy is known to solve arbitrarily complex obstacles (Kamon and Rivlin 1997). Multiple strategies exist that are extremely robust, but all require more information processing than Simple 1.</td>
</tr>
<tr>
<td>Extremely robust 2</td>
<td>Groups follow the “extremely robust 1” described above, but if they navigate over ground they have already moved over, they abandon the transport effort. This requires detecting when they move over their footsteps, which can be accomplished through path integration, for example.</td>
<td>Groups will successfully navigate both the wall and the cul-de-sac with sinuosity = 1 for each. This strategy also succeeds in the trap because individuals can give up, moving on to other useful behaviors.</td>
</tr>
<tr>
<td>Intermediate strategies</td>
<td>There are many possible strategies that would lead to moderately robust navigation. All require more information than the simplest strategy. Using trajectory data, we can infer properties of the strategy.</td>
<td>Groups succeed at both the wall and the cul-de-sac. Efficiency for the wall may be higher (lower sinuosity) than for the cul-de-sac. Efficiency is lower than an extremely robust strategy (sinuosity &gt; 1) for both obstacles.</td>
</tr>
</tbody>
</table>
We investigate obstacle navigation during cooperative transport in *Paratrechina longicornis* (Latreille), the longhorn crazy ant. Workers of this species are known to be excellent transporters (Czaczkes et al. 2013; Gelblum et al. 2015). *P. longicornis* is in the subfamily Formicinae and is a widely distributed “tramp” ant (Wetterer 2008). We presented groups of ants with obstacles of varying difficulty in order to look at the navigation strategy they use, and where their strategy falls between simple and robust problem solving. We obstructed ant cooperative transport groups with three increasingly complex obstacles: an obstacle that simple strategies can easily navigate (the “wall”), an obstacle that requires a more robust strategy (the “cul-de-sac”), and an impossible obstacle that thwarts even robust strategies (the “trap”) (Figure 6.1). Example strategies with their predictions are shown in Table 6.1. Our main questions were: 1) How robust is the strategy of groups of ants? 2) What strategy do the ants use? 3) How do individuals contribute to the group’s strategy? 4) When facing an obstacle that is impossible to navigate, do groups have the ability to detect traps, and if so what is their response?
6.3 METHODS

Overview

We gave ants foraging near a colony entrance pieces of tuna to carry. After a group of ants had begun carrying the tuna, and their preferred direction of travel was established, we put one of three obstacles in their path, directly blocking that preferred direction. We video recorded these trials and extracted data from the videos, including the trajectory of the piece of tuna, which we used to measure additional results metrics, described below.
For question 1, we examined strategy robustness by looking at which obstacles groups of ants could navigate, their efficiency at the wall and the cul-de-sac, and how well they maintained consensus about travel direction (Table 6.1). For question 2, we identified behavioral elements (e.g. perimeter following) that make up the strategy. For question 3, we examined individual behaviors during key decisions in obstacle navigation, to look for precipitating events such as ants joining. For question 4 we compared group behavior in the cul-de-sac and the trap.

Study sites

We conducted fieldwork in June 2014 at two sites: Arizona State University in Tempe, Arizona, and the Biosphere 2 facility in Oracle, Arizona, using two colonies in Tempe and two at Biosphere 2 (4 colonies total). We worked in locations having a flat surface, with relatively constant shade, and close to only one nest entrance so that all foragers had the same goal. The general pattern of navigation behavior, including strategy, was similar among these four colonies.

Obstacles and strategy

We used three types of obstacles. 1) The simplest obstacle (Figure 6.1A), hereafter referred to as the “wall,” requires a form of symmetry breaking: groups must choose a direction from equal options. We placed obstacles approximately perpendicular to groups’ travel direction, blocking the nest direction. Two of the remaining options (left and right) are of equal value, so a choice between them requires breaking symmetry. 2) A complex obstacle (Figure 6.1B), the “cul-de-sac,” also requires symmetry-breaking, but has an additional challenge. Groups navigating this obstacle must move opposite to their preferred direction (away from the nest) to
succeed. The last obstacle (Figure 6.1C), the “trap,” resembles the cul-de-sac but is impossible to navigate. However there are strategies that would allow groups to know that they are trapped. In natural settings, such strategies are more robust, because if groups recognize that navigation has failed, individual ants can abandon the transport and switch to other behaviors. For example, without their load, ants may be able to escape and return to the nest.

Navigation strategies are also of interest in robot navigation, and a substantial body of literature predicts the consequences of various navigation strategies in the presence of obstacles of varying complexity (Lumelsky and Stepanov 1987; Kamon and Rivlin 1997; Murphy 2000). While we do not expect ants to use any specific strategy from this literature, we used these predictions to design our obstacles, so that we know a strategy that can solve each one. We compared the ant groups’ trajectories to the predictions for these theoretical strategies, listed in Table 6.1. Groups without a navigation strategy fail to reach consensus if obstructed. In the “Simple 1” strategy groups follow the perimeter of an obstacle and move toward the nest if possible. This strategy succeeds at the wall, but fails at the cul-de-sac. Groups using the “Extremely robust 1” strategy follow the perimeter of an obstacle until they can move toward the nest, and they are also closer to the nest than they have previously been. This strategy is efficient for both the wall and the cul-de-sac, but groups using this strategy in the trap will continue attempting to navigate it indefinitely. In the “Extremely robust 2” strategy, groups use the same rules as the “Extremely robust 1” strategy, but additionally they abandon navigation if they travel where they have already been. This allows groups to detect that they are trapped. Strategies that succeed with a wider range of obstacle types require more information processing than simpler strategies (Table 6.1). The strategies included here are just examples; the range of potential strategies is large, and strategies could include more stochasticity. For example, groups may
follow the perimeter of an obstacle until the nest direction is available, at which point they move toward the nest with some probability, otherwise continuing to follow the perimeter. Stochastic strategies may allow groups to navigate a wider range of obstacles, but their efficiency with a given obstacle will be different in each encounter.

All potential strategies are composed of behavioral elements. Examples of elements included in the strategies in Table 6.1 are perimeter following, moving toward the nest, moving away from the nest, and remembering the path travelled. Other possible elements include spontaneous direction changes and random walks.

Experiment details

At the beginning of each trial, a fresh piece of 11x17 inch (28x43 cm) white paper was placed on a flat surface near a nest entrance. We set up in locations where all successful foragers returned to the same entrance, to ensure that individuals in our transport groups would have the same goal. The nest entrance was at least 15 cm away from our experiment. At the start of each trial a dead cricket was placed on the paper, so that foragers would recruit by laying pheromone. We used a cricket to elicit a strong recruitment response, so that transports would not fail because of insufficient workers. When a group of workers began moving the cricket, we replaced it with a marked piece of tuna, lighter than the cricket (0.031 g - 0.105 g). Once a group of workers had moved the tuna at least 10 cm, one of the obstacles was placed in their path, oriented such that the “back wall” (dashed red line in Figure 6.1) was perpendicular to their preferred direction. For the trap, we first obstructed their path with an obstacle shaped like the cul-de-sac. After the group entered this obstacle, we placed a “door” in the exit to trap groups. We ended trap trials after 12 minutes; this was more than sufficient to capture group behavior.
We did not try to eliminate additional ants from being in the vicinity of the transport effort. These “extra” ants, also known as escorts, are common in natural *P. longicornis* transport efforts (Czaczkes et al. 2013), and whatever affect they have on navigation would also be present in natural navigation efforts.

These escort ants did not alter pheromone trails to help groups navigate around obstacles. *P. longicornis* workers lay a specialized pheromone trail to recruit ants to a large item, but cooperative transport groups do not use that trail to navigate back to the nest (Gelblum et al. 2015). The recruitment trail is short-lived, decaying within 6 minutes (Czaczkes et al. 2013), and workers laying this trail have a conspicuous, halting movement pattern which we did not observe during navigation. Instead of relying on a pheromone trail, recent studies suggest that transport groups in *P. longicornis* can be aided in returning to the nest by new ants joining the effort (Gelblum et al. 2015). To rule out the possibility that other workers provide another type of global directional cue, we conducted an experiment to see how long an obstacle must be in place before ants avoid it altogether. In our experiment, the vast majority of ants moving from sugar-water baits toward a nest initially hit the obstacle we placed in their path, but eventually ants’ paths changed so that they avoided the obstacle. However, this change took over 20 minutes, while our longest trial was only 10.8 minutes (Appendix 6-4). Over the length of time that our trials lasted, ants’ paths had not substantially changed to avoid obstacles. Escort ants may yet provide cues to cooperative transport groups through physical contact or another mechanism, but it is unlikely that they provide global cues conveying directional information.

All trials were recorded using a Canon Rebel T2i with lens EF-S 18-55IS (1920x1080, 30 frames per second; Canon, Tokyo, Japan). All obstacles were constructed out of Lego® (Billund,
Denmark) and coated on the inside with Insect-a-Slip (Fluon; BioQuip, Gardena, CA, U.S.A.) to prevent groups climbing over them.

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

**Data extraction**

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

*Speed:* We used speed to evaluate how well groups maintain consensus (for question 1) and to compare group behavior in the cul-de-sac and the trap (question 4). Because group size and speed were correlated (see results), we also used speed to evaluate how individuals affect efficiency (question 3). Speed was measured every second, so it approximates instantaneous speed. When the speed was extremely low (less than 0.048 cm s\(^{-1}\)) we classified the group as being “stalled.” For analyses in which we compared speeds across trials, we eliminated speed data for times until the group first reached a threshold speed of 0.24 cm s\(^{-1}\).
**Sinuosity**: Sinuosity is defined as the ratio of the path length to length of the shortest path. Paths with lower sinuosity are more efficient. We used sinuosity to compare navigation efficiency among obstacles (question 1). Here, in order to directly compare obstacles, we used a modified measure of sinuosity: the path length divided by the path that would be taken if groups followed the perimeter of the obstacle (Figure 6.1A,B).

**Backward runs**: For the cul-de-sac, successful navigation requires moving away from the nest. We evaluated the extent to which groups did this by quantifying the number and distance of “backward runs.” A backwards run is a period of time during which the group is moving away from the nest (and away from the back wall). Backwards runs occur when the distance from the tuna to the back wall is increasing, and the run ends when this distance decreases. For each backwards run we recorded the time at which the run started, and the displacement away from the back wall that occurred during that run. Analyzing backwards runs provided insight into strategy elements (question 2) and we also compared backwards runs in the cul-de-sac and the trap (question 4).

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

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

In addition to these results metrics that we measured from group trajectories, we manually measured navigation time (for question 1) and group size (for question 3). For navigation time, we defined the start of navigation as when a group first appeared to respond to the “back wall,” and we defined the end of navigation as when they rounded one of the bottom corners (colored in solid red in Figure 6.1). To find group size we counted the number of ants attached to the tuna every 15 seconds.

**Statistical Analysis**

All statistical analyses were performed in R, version 3.2.2 (R Core Team 2015).

**Question 1: How robust is the navigation strategy of groups of ants?** We compared efficiency data in the wall and the cul-de-sac with a $t$-test on sinuosities, log-transformed to meet
assumptions of normality. To look at how well groups maintain consensus, we compared stalls and speeds while groups were navigating and while unobstructed. The proportion of time groups were stalled was analyzed with a Bayesian zero-inflated beta model using Stan implemented in R (Stan Development Team 2015). We chose this method because these data were heavily zero-inflated, such that general or generalized linear models were inappropriate. We used a binomial model to examine the probability of never stalling, and for trials with at least one stall, we used a beta model to look at the proportion of time stalled. We evaluated the effect of potential predictors on this proportion, but not on the probability of never stalling, because this probability is biased among obstacles: groups are less likely to never stall in the cul-de-sac because it takes them longer to navigate it. Priors were relatively vague and did not substantially impact posteriors.

We used general linear models to analyze square-root transformed speeds using the lme4 package (Bates et al. 2015). Transformed speeds were normally distributed. As potential predictor variables, we included whether the group was navigating an obstacle or unobstructed, and which obstacle was navigated. We compared a full model with both predictors and their interaction to simpler models with one or both predictors without the interaction (Appendix 6-1). We also included random effects of trial nested within colony. We compared models with Akaike Information Criteria (AIC) to determine the best predictor variable(s).

**Question 2: What strategy do groups use?** We qualitatively examined trajectories to identify strategy elements. To examine how backward movements contribute to strategy, we analyzed distances of backward runs in a Bayesian framework using JAGS in R (Plummer et al. 2015). We saw how behavior changed over time by modeling the distribution of backward runs
distances as a gamma distribution, where the shape parameter, k, can change in time according to the following equation.

\[ k = e^{\alpha_i + \beta t} \]

Where \( \alpha_i \) represents a random intercept for each trial and \( \beta \) indicates the extent to which \( k \) changes over time. Gamma distributions with larger shape parameters are more right-skewed.

We also fit additional parameters indicating the scale of the beta distribution and the mean and standard deviation of \( \alpha_i \). We verified this model by simulating hundreds of data sets and checking that the 95% credible interval included the true parameter 95% of the time. We looked at whether the distribution of backward run distances changes over time by evaluating whether \( \beta \) is different from zero. Our priors did not substantially impact posteriors. To avoid bias in the timing of large backwards runs, we excluded any backward run that led to the group completing obstacle navigation.

**Question 3: How do individuals contribute to the group’s strategy?** In addition to a qualitative analysis of sharp turns and escape points, we examined the effects of group size and speed on performance using Pearson product-moment correlations, with log-transformed data where necessary. We also looked at the effect of group size on speed and on the number of turns using Kendall rank correlations, as speed data and number of turns in each trial could not be transformed appropriately for a Pearson correlation due to non-normality. These analyses allow us to see how individuals affect efficiency through group size.

**Question 4: How do groups behave with an impossible obstacle?** To see how group behavior differs in the trap and the cul-de-sac, we qualitatively analyzed speed and group size over time in these obstacles. We used the ggplot2 package (Wickham 2009) to visually compare these metrics, smoothing the speed data with local regression (LOESS) or generalized additive
models (GAM), depending on the number of observations. We also compared stalls and backwards runs in the cul-de-sac and the trap, using statistical tests described above.

6.4 RESULTS

1) How robust is the navigation strategy of groups of ants?

*P. longicornis* groups successfully navigated both the wall (n = 22) and the cul-de-sac (n = 19) in every trial. Examples of groups’ trajectories are shown in Figure 6.2 (Appendices 6-5, 6-6, and 6-7 show group trajectories for all trials). The mean times to navigate the obstacles were 1.01 minutes (*s.e.m.* = 0.17) for the wall and 5.99 minutes (*s.e.m.* = 0.52) for the cul-de-sac, with a mean speed across trials of 0.43 cm s\(^{-1}\). While groups always solved both obstacles, they were significantly more efficient solving the wall than the cul-de-sac, (untransformed sinuosity means: 2.5 (*s.e.m.* 0.36) and 6.3 (*s.e.m.* 0.80); unpaired *t* test, *t*\(_{39}\) = 5.05, *P* < 0.0001; Figure 6.3).

We also looked at how well groups maintain consensus. We expect groups lacking consensus to stall. Transport groups rarely stalled (< 2% of the time) either while navigating obstacles or while unobstructed (Table 6.2). Groups had a 54% chance of never stalling (probability = 0.54, 95% credible interval (CI): 0.43 – 0.64). For trials in which at least one stall occurred, groups spent the same proportion of time stalled regardless of whether they were obstructed. Posterior distributions overlapped substantially for unobstructed groups (mean = 0.044, 95% CI: 0.025 – 0.081), groups navigating the wall (mean = 0.044, 95% CI: 0.021 – 0.084), and groups navigating the cul-de-sac (mean = 0.025, 95% CI: 0.014 – 0.052). We estimated random intercepts for each colony, but found that colonies did not differ in proportion of time stalled (Appendix 6-8). The results show that groups rarely stall, and the proportion of time groups are stalled is not affected by either the wall or the cul-de-sac.
Figure 6.2: Examples of group trajectories. Warmer colors indicate early points in the navigation process, while cooler colors are later in time. A, B: the wall; C, D: the cul-de-sac; E, F: the trap. Times shown in the bottom right corner of each panel indicate the time it took to navigate the obstacle (from hitting the back wall to rounding the corner) for A through D, and the time spent trapped for E and F.
**Figure 6.3:** Efficiency (sinuosity) of cooperative transport for groups navigating the wall (n = 22) and cul-de-sac (n = 19). Unpaired $t$ test, $t_{39} = 5.05$, $p < 0.0001$. Large dots show jittered sinuosity values for each trial. Letters indicate groups are significantly different. Boxes include 50% of the data (going from the 25th to 75th percentiles), and whiskers extend to the lowest and highest values that are within 150% of the interquartile range. Small dots are points outside that range.

**Table 6.2:** Proportion of time spent stalled while unobstructed (before or after obstacle navigation) and during obstacle navigation. Values shown are means of these proportions for each trial, including trials with zero stalls. Standard errors are shown in parentheses.
To look further at consensus, we evaluated the effect of obstacles on speed using general linear models. The best model included whether the group was obstructed ($\beta = -0.065$), and did not include whether they were navigating the wall or the cul-de-sac. Detailed results of this best-fit model are included in Appendix 6-2. Groups slow down while navigating obstacles and this effect is not different for different obstacles. However, the effect size was small; all else being equal, groups moved only 0.043 cm s$^{-1}$ slower while navigating obstacles. This is approximately a 10% reduction in speed, and this decrease is much smaller than the overall variation in speeds of groups (Appendix 6-9).

2) What strategy do groups use?

We looked at elements – the behavioral components of strategy – to answer this question. The primary challenge in navigating the wall is to break symmetry. We could not ensure perfect symmetry among the options for travel direction (obstacles were not always perfectly perpendicular to preferred direction), but groups did not favor the direction closer to their initial travel direction. Upon hitting the wall, $P. longicornis$ groups broke symmetry, choosing a single direction to move around it. They did not, however, stick with that chosen direction for the entire navigation. In 14 out of 22 trials (64%), the group changed direction after the initial choice. The groups also navigated directly up to the wall, and typically remained close to the wall perimeter after choosing a direction (Figure 6.2 Appendix 6-5). There was no visual detection and evasion; transport groups did not avoid any of the obstacles.

The cul-de-sac presents an additional challenge in that groups must move counter to their preferred direction. Initial behaviors of groups in the cul-de-sac were similar to those of groups navigating the wall; transport groups first hit the back wall of the obstacle and quickly picked a
direction. Early in the navigation process, groups remained close to the back wall, but they did not typically move along the side walls (Figure 6.2). Later in the navigation process groups moved away from the perimeter into the open area within the cul-de-sac. Our results show that in the cul-de-sac, groups moved further backwards (away from the nest) the longer they had been navigating (Figure 6.4). More specifically, the distribution of distances of backwards runs becomes more right-skewed (shifted toward longer distances) over time. Our estimate of \( \beta \) in the cul-de-sac is 0.13, and the 95\% credible interval (CI) is 0.07 – 0.20. We did not find strong evidence for this effect in the wall (\( \beta = 0.0019, \) 95\% CI: -0.15 – 0.15, Appendix 6-10A), perhaps because groups navigated the wall rapidly. Transport groups change their behavior over time. Estimates for all parameters for this analysis are in Appendix 6-3. Descriptions of observed strategy elements are included in Table 6.3.

**Figure 6.4:** Densities of backward run distances of groups navigating the cul-de-sac at different time intervals. A: All backwards runs data for the cul-de-sac; B: same data as panel A, but zoomed in to show only backwards runs 5 cm or less. Modeled in a Bayesian framework as a gamma distribution with a changing shape parameter, our estimate of the effect of time, \( \beta \), is 0.13 (95\% CI: 0.07 – 0.20). In the cul-de-sac, the distribution of distances of backwards runs becomes more right-skewed over time.
Table 6.3: *P. longicornis* strategy elements for obstacle navigation.

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

3) *How do individuals contribute to the group’s strategy?*

We observed many sharp turns during these experiments, yet stalls were rare. Thus, groups were able to sharply change direction without stalling. We qualitatively examined the sharpest turns made while navigating the wall (n = 38). In 32% of cases the change in direction appeared to be caused by a new ant joining the group, in 24% of cases the group hit the obstacle, and in 45% of cases we could see no event precipitating the direction change (Table 6.4). We conducted a similar analysis of escape points in the cul-de-sac (Table 6.4). In over half of cases (58%) we could detect no events that seemed to cause the direction changes leading to escape, while 32% were caused by new ants.
Table 6.4: Apparent reasons for the sharpest turns during wall navigations (n = 38), and for the last turn leading to escape from the cul-de-sac (n = 19).

<table>
<thead>
<tr>
<th></th>
<th>Ant joined</th>
<th>Ant left</th>
<th>Hit obstacle</th>
<th>No discernable reason</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sharp turns</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number (out of 38)</td>
<td>12</td>
<td>0</td>
<td>9</td>
<td>17</td>
</tr>
<tr>
<td>Percent</td>
<td>32%</td>
<td>0%</td>
<td>24%</td>
<td>45%</td>
</tr>
<tr>
<td><strong>Escape points</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number (out of 19)</td>
<td>6</td>
<td>2</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Percent</td>
<td>32%</td>
<td>11%</td>
<td>0%</td>
<td>58%</td>
</tr>
</tbody>
</table>

In addition to individual contributions at key moments, we looked at what effect group size had on transport efficiency. Within the range of group sizes we observed, transport groups with more ants were faster: Number of ants and speed were correlated (Kendall’s $\tau = 0.44$, $P < 0.0001$). This correlation was present within colonies as well as in the pooled data (Appendix 6-11). However, groups navigating the wall with higher average speeds were not more efficient with respect to sinuosity (Pearson’s $r = -0.14$, $P = 0.53$; Figure 6.5A). Furthermore, for the cul-de-sac, faster groups were less efficient, in that they had higher sinuosity (Pearson’s $r = 0.62$, $P < 0.01$; Figure 6.5B). This correlation in the cul-de-sac was present across colonies, but not within individual colonies. Colonies at Arizona State University tended to have higher speeds and sinuosities, while colonies at Biosphere 2 tended to have lower speeds and sinuosities (Figure 6.5B). Groups with more ants were not more efficient with respect to sinuosity (wall: Pearson’s $r = -0.18$, $P = 0.43$, cul-de-sac: Pearson’s $r = 0.25$, $P = 0.30$, Appendix 6-12A,B), and did not change directions more frequently than smaller groups (wall: Kendall’s $\tau = -0.19$, $P = 0.25$, cul-de-sac: Kendall’s $\tau = 0.17$, $P = 0.36$, Appendix 6-12C,D).
**Figure 6.5:** Mean speed of groups is not correlated with sinuosity for groups navigating the wall (A; Pearson’s $r = -0.14$, $P = 0.53$), and is positively correlated with sinuosity for groups navigating the cul-de-sac (B; Pearson’s $r = 0.62$, $P < 0.01$). Blue dots are points for colonies at Arizona State University (light blue: colony LA; dark blue: colony LD) and green dots indicate colonies at Biosphere 2 (light green: colony LM; dark green: colony LS).

4) **How do groups behave with an impossible obstacle?**

Groups in the trap behaved starkly differently from groups in the cul-de-sac, across multiple results metrics. We expected groups to behave similarly in the trap and the cul-de-sac at least initially, however groups’ speeds in these obstacles differ even early in the navigation process, with groups in the trap slowing down dramatically (Figure 6.6). This drop in speed corresponds to a reduction in group size (Appendix 6-13), and an order-of-magnitude increase in the amount of time groups are stalled (Table 6.2). Furthermore, while our analysis of backwards runs indicates that groups have larger backwards runs the longer they have been in the cul-de-sac, we found the opposite pattern for the trap ($\beta = -0.22$, 95% CI: -0.26 – -0.19, Appendix 6-10C). This likely results from groups moving more slowly and less. In the trap, over time, groups explore the space less and less.
Figure 6.6: Speeds of groups over time navigating the cul-de-sac (A) and in the trap (B). Groups in the trap reduce their speed dramatically, while groups in the cul-de-sac maintain relatively constant speeds. Light grey, unsmoothed lines (background) show raw speed data. Grey, smooth lines show the smoothed speed for each trial, computed with LOESS, and black lines show smoothed speed across trials, computed with GAM.

6.5 DISCUSSION

We presented *P. longicornis* cooperative transport groups with obstacles that require a series of decisions to navigate (problem solving). From their responses we infer what kind of strategy they use. We predicted a simple strategy based on nest direction would fail at the cul-de-sac, while an extremely robust strategy would be maximally efficient (sinuosity = 1) for both the wall and the cul-de-sac. Neither of these extreme results occurred. Instead, *P. longicornis* uses a moderately robust strategy. Groups of ants were more efficient – took more direct paths in less time – when navigating the wall than the cul-de-sac (Figure 6.3), but groups still always succeeded in solving the cul-de-sac. Furthermore, their strategy was stochastic. Trajectories differed greatly from one trial to the next, and groups did not respond predictably when facing a given set of circumstances. While we do not know exactly how robust their strategy is, we show
that it is more robust than one based only on nest direction (e.g. the “Simple 1” strategy).

Furthermore, because they are more efficient at the wall than the cul-de-sac, we can rule out the “Extremely Robust” example strategies in Table 6.1. In terms of the trade-off between simple, inexpensive strategies that may fail and robust strategies that require more information, this ant species appears to have a solution that lies in between. They can navigate complex obstacles, but not without some cost in terms of efficiency.

In addition to showing that groups can navigate complex obstacles we were also able to determine how they succeed. Groups have stochastic behavior that changes over time. Early after encountering an obstacle, groups were unlikely to move substantial distances “backwards” (away from the nest). This is consistent with groups initially using a simple strategy in which they move in the nest direction whenever possible. This strategy was successful with the wall but not with the cul-de-sac. Groups navigating the cul-de-sac gradually changed their behavior by incorporating longer backwards movements, allowing them to find the exit. If groups had incorporated many backwards runs from the beginning, it would have taken them longer to navigate the wall. Thus, changing their strategy over time allows them to rapidly solve simple obstacles, while still eventually succeeding at complex ones.

Regardless of the specific obstacle being navigated, groups were highly effective at maintaining consensus while making serial decisions. These groups chose an initial travel direction after encountering the obstacle, and also frequently decided to change direction. They decided to move backwards or they decided to move toward the nest again. When groups changed direction, they did so rapidly, without stalling, as the proportion of time stalled was the same whether or not they were obstructed. Stalls were also rare unless they were trapped (Table 6.2), and their speed was only slightly reduced while navigating obstacles. In the absence of
obstacles, maintaining consensus is easier because groups simply move toward the nest. We conclude that transport groups are capable of maintaining consensus even when the nest direction is blocked.

How were groups able to maintain consensus, especially while changing direction? In some cases, direction changes that led to escape seemed to be initiated by new ants joining the transport effort (Table 6.3). These new ants may have more information about the shape of the obstacle, and will have arrived using a successful path. Compliance is important in consensus decisions, and if groups rapidly conform to a new individual, as Gelblum et al. (2015) reported, they are likely to succeed. Indeed, we found that in 32% of cul-de-sac trials, the initiation of the escape turn coincided with a new ant joining the group. Yet in the remaining trials no new ant was present, and in 58% of cases we could see no cause for the change. For the sharpest turns we again observed that while a substantial portion of turns coincided with new ants joining (32%), in almost half of cases (45%) we detected no event precipitating the change. Yet these changes occurred rapidly without stalling. We concur with the conclusion of Gelblum et al. (2015) that these groups rapidly conform to newly imposed directions, and we add that in the case of obstacle navigation, these new directions do not need to come from new group members. Existing group members may also impose new directions. They may do so randomly, although this suggests that larger groups change direction more frequently, which we did not find across the relatively small range of group sizes we observed. Group members may also impose new directions because of new information they have received, perhaps from unladen ants not interacting with the object. A highly conforming group may rapidly change direction based on cues from a single individual, whether or not that individual has recently joined the group.
Groups changed direction frequently, often with no clear external cue for doing so. In some cases these direction changes appeared counter-productive, occurring just before the group would have reached the end of the wall (Figure 6.2A,B). Could occasional spontaneous direction changes be beneficial? Assuming groups do not know the shapes of obstacles they navigate, direction changes allow for flexibility and could prevent extraordinarily long navigation times. Consider an obstacle shaped like a very long wall. A group may happen to encounter this obstacle close to the left end, but initially turn right to navigate around it. If they never change direction they will have to traverse nearly the entire length of the wall. On the other hand, if they spontaneously change direction they will find the end relatively quickly. Thus, these spontaneous direction changes allow groups to abandon unsuccessful tactics and try new, potentially fruitful, directions.

In addition to spontaneous direction changes, we observed other strategy elements used by *P. longicornis* (Table 6.3). Both obstacles require symmetry breaking: after encountering the obstacle groups must choose a travel direction from equal options. In every trial, groups quickly broke symmetry. Groups also followed the perimeter of the obstacle – with few exceptions groups navigating the wall remained close to the obstacle (Appendix 6-5). This may simply result from groups being unlikely to move away from the nest. Likewise, groups in the cul-de-sac initially stayed close to the back wall, but typically did not continue following the perimeter to travel “backwards” along the sides of the obstacle. Yet the longer a group was in the cul-de-sac, the more time they spent moving away from the nest. Even then, spontaneous direction changes were always present; direction changes were initially constrained mainly to movement along the back wall, while later, direction changes were less constrained resulting in a more complete exploration of the space.
These observations give us a partial picture of the group strategy, which initially includes symmetry breaking, moving toward the nest when possible – resulting in perimeter following, and spontaneous direction changes. If the group remains unsuccessful, their behavior changes to include less perimeter following and incorporating a new element: moving “backwards.” By investigating how these elements are implemented, future studies could elucidate more about the mechanisms of collective problem solving.

We also investigated the effect of group size on transport and navigation. We found that larger groups moved faster than smaller groups, which agrees with analyses presented by Gelblum et al. (2015). Surprisingly, while larger groups had faster speeds, the increase in speed did not result in faster obstacle navigation. In fact, in the cul-de-sac, faster groups are less efficient. Specific colonies tended to be either relatively slow with low sinuosities or relatively fast with high sinuosities (Figure 6.5B).

While most of our analysis focused on the wall and the cul-de-sac, we also found some unexpected behavior for groups in the trap. The shape of the cul-de-sac and trap only differ by whether or not there is an exit. We expected trapped groups to behave similarly to groups in the cul-de-sac for at least as long as it took to navigate the cul-de-sac, after this time it is reasonable to imagine that groups may stop trying. Instead, we found that groups have dramatically different behavior in the trap, and the difference is apparent right away. Groups slowed down quickly, and group size decreased as individuals spent less time grasping the object being carried. This suggests that these ants are capable of detecting that they are trapped, or at least detecting a difference in their situation compared to the cul-de-sac.

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

Overall, our results demonstrate that *P. longicornis* employ a problem solving strategy that adapts to the complexity of the problem. Future work should aim to understand how this strategy is implemented. How do groups maintain consensus? Perhaps a quorum is required for decisions, as in nest site selection in honey bees and *Temnothorax* (Pratt 2005; Seeley 2010), or perhaps informed individuals play an outsized role in decisions (Couzin et al. 2005; Gelblum et al. 2015). How is information integrated and transferred within the group? Information may be transferred through the object itself (Kube and Bonabeau 2000; McCreery and Breed 2014), or maybe escorts aid information transfer. This study focused on *P. longicornis*; other species that are effective at cooperative transport, such as *Novomessor cockerelli*, may have evolved completely different strategies. Understanding the range of strategies employed by ant species would lead to new insights into the information processing and collective problem-solving strategies of ants.
Our study also has implications for collective problem solving in other animals. Many animals navigate in groups, from schools of fish to large migrations, and these groups must form consensus to remain cohesive. We show that a group reliant on consensus can collectively make a series of stochastic decisions in order to navigate a complex, unknown environment. In addition, obstacle navigation strategies in \textit{P. longicornis} may provide inspiration for the design of new stochastic strategies for robotics (Bonabeau and Théraulaz 2000). Ant collective behavior has been a rich source of concepts for research in distributed algorithms, including for cooperative transport by robots (Berman et al. 2011; Rubenstein et al. 2013), and insights from effective social groups like \textit{P. longicornis} could provide new ideas for designing robot teams that robustly tackle complex environments. Indeed, we show that \textit{P. longicornis} groups are able to collectively navigate complex environments by using a cohesive, flexible, and robust navigation strategy.
Cooperative transport is an ideal task for studying collective behavior and collective intelligence for two reasons. First, to succeed, groups must perform sub-tasks – such as deciding on travel direction, and maintaining consensus throughout transport – that are commonly required in other tasks. Second, ant species vary widely in how efficient they are at cooperative transport, allowing one to determine which traits contribute to collective intelligence by comparing among species. A few ant species quickly transport objects many thousands of times the mass of an individual (Wojtusiak et al. 1995; Gelblum et al. 2015; Fonio et al. 2016), while other species fail to coordinate their efforts. My dissertation focused on discovering the mechanisms that allow some species to succeed at cooperative transport, and I especially focused on two difficult challenges: forming consensus about travel direction and navigating around obstacles. The main questions and findings of my dissertation are summarized in Table 7.1.
Table 7.1: Main questions and conclusions of Chapters 3 through 6 of the dissertation. Not included in this table is Chapter 2, which presents a overall framework for cooperative transport research, including descriptions of four phases of transport. Chapters are organized by the major challenge they deal with (collective decision or problem solving), and by whether they focus primarily on individual- or group-level mechanisms.

<table>
<thead>
<tr>
<th>Primary question(s)</th>
<th>Selected findings</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Collective decision about travel direction</strong></td>
<td></td>
</tr>
<tr>
<td>Group level</td>
<td></td>
</tr>
</tbody>
</table>
| *Chapter 3:* How do object properties affect cooperative transport success in *P. longicornis*? | • Object size and mass per ant affect speed and coordination time, but not the maintenance of coordination  
• For a given mass per ant, groups carrying larger objects take longer to begin moving, but move faster |
| Individual level | |
| *Chapter 4:* What are the theoretical consequences of individual traits for deadlocks? | • Even groups of simple individual can break deadlocks, if individuals perceive whether they are aligned with the majority  
• Groups coordinate quickly with either a shared directional bias, high sensitivity to group behavior, or finely tuned persistence |
| Individual level | |
| *Chapter 5:* Does individual persistence promote group consensus? | • Species with more persistent individuals form more coordinated groups  
• Artificially increasing persistence in groups increases coordination |
| **Problem solving: How to navigate around obstacles?** | |
| Group level | |
| *Chapter 6:* Can *P. longicornis* groups implement a collective obstacle navigation strategy? How robust is that strategy, and what elements does it include? | • Groups of *P. longicornis* maintain remarkably good consensus while navigating around difficult obstacles  
• Groups implement a flexible, robust navigation strategy, incorporating more complexity the longer they are stuck  
• Elements include moving toward the goal, symmetry breaking, perimeter following, spontaneous direction changes, and moving “backwards” under certain circumstances |
| Individual level | |
| *Chapter 6:* How do individuals joining *P. longicornis* transport groups contribute to important strategy decisions? | • One third of the sharpest group turns and the turns that led to escape during obstacle navigation coincided with a new ant joining the group, but in about half there was no discernible reason for the change  
• Many important navigation strategy decisions are implemented without apparent external input |
My review of cooperative transport mechanisms (Chapter 2), introduced a framework for understanding the process of cooperative transport including four phases: decision, attraction or recruitment, organization, and transport. I made the case for using common measures of cooperative transport efficiency, to enable cross-species comparisons, and I presented hypotheses for individual traits and mechanisms that may affect group coordination.

I presented three chapters focusing on the first transport challenge: that groups must form consensus about travel direction to succeed. In Chapter 3, I examined the effect of object mass and size on success during the beginning of transport at the group level. I discovered that in the species *Paratrechina longicornis*, transport attempts in which each ant must carry more (higher mass per ant) lead to longer coordination times and lower speeds, but the maintenance of coordination (sinuosity) is not affected. Object size also affects coordination time and speed, but in opposite directions. At the individual level, I examined the collective decision about travel direction in Chapters 4 and 5. In Chapter 4, I presented a theoretical study showing that even groups of simple individuals, with no memory and limited information, can break deadlocks. Individuals must only determine whether they are aligned with the majority. While real ants have more capabilities than my simulated ants, including memory, they do not need those capabilities to break deadlocks. I also examined the individual trait persistence in this theoretical project. While I had expected high individual persistence to reduce coordination (see Chapter 2), my theoretical results suggested the opposite effect. I tested the effect of persistence empirically in Chapter 5, and these results agreed with the theoretical conclusions. Species with more persistent individuals form more coordinated groups, and artificially increasing the persistence in groups increases their coordination.
Groups that succeed at forming a consensus about travel direction must overcome an even more difficult challenge: navigating around obstacles in their environment. In Chapter 6, I present a group-level study exploring obstacle navigation and problem-solving strategies in *P. longicornis* groups. There is a tradeoff in terms of strategy, between simple strategies that are easy to implement but fail at some obstacles, and more difficult strategies that will succeed in more situations. I found that *P. longicornis* groups maintain consensus while using a flexible strategy that is initially simpler, and rapidly solves simple obstacles, but incorporates more complexity if the group remains unsuccessful, allowing groups to succeed at more difficult obstacles. This collective problem solving strategy is flexible, robust, and implemented at the group level.

Like other examples of collective, or swarm, intelligence (Dorigo et al. 2006; Garnier et al. 2007), ants that succeed at cooperative transport do so with decentralized control. I have contributed to our understanding of mechanisms that allow for this success by conducting both theoretical and empirical experiments, and by examining mechanisms both at the individual group levels. In the case of cooperative transport, my work tests how individual traits and behaviors lead to emergent group behavior, which is an important question for emergent phenomena across all scales in nature. I have discovered specific individual traits that promote emergent behavior. I have shown that *P. longicornis* ants have at least one of these traits, and they excel at group decisions. Finally, I have demonstrated that, at the group level, *P. longicornis* workers implement a collective problem solving strategy. This work elucidates cooperative transport in ants, suggests mechanisms to improve cooperative transport in robots, and more generally, it enlightens the mechanisms of collective intelligence and emergent group behavior.
REFERENCES


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APPENDIX

Appendix 4-1: Analysis of deadlock stability in informed case

We used fixed-point analysis to analytically investigate the stability of deadlocks in the informed case (Strogatz 1994 Section 6.3, also described elsewhere). First, we found the location of the fixed point (equilibrium) in terms of $N_L$ and $N_R$. The fixed-point is the location where the time derivatives of $N_L$ and $N_R$ are equal to zero. We found that the fixed point occurs at the following values of $N_L$ and $N_R$:

$$N_L^* = \frac{2 J_L N_{total}}{b_1 + 4 J_L}, \quad N_R^* = \frac{2 J_R N_{total}}{b_1 + 4 J_R}$$

where $N_L^*$ and $N_R^*$ are the specific values at the fixed point. $J_L$ and $J_R$ are the transition rates for individuals moving from the disengaged group to the “moving left” and “moving right” groups, respectively. We made the simplification that $N_L = N_R$ to examine only the case of a deadlock. Note that this condition of $N_L^* = N_R^*$ is only satisfied if $J_L = J_R$. Thus, deadlocks with equal numbers in each group only occur with no directional bias.

Next, we performed a first order Taylor expansion around the fixed point, with $\Delta = \begin{pmatrix} \Delta_1 \\ \Delta_2 \end{pmatrix}$ as a perturbation, where $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$ and $\begin{pmatrix} 0 \\ 1 \end{pmatrix}$ are the $N_L$ and $N_R$ directions, respectively. The equations of motion for $\Delta$ are:

$$\frac{d \Delta_1(t)}{dt} = - \frac{\left( b_1^2 + 8 J^2 + b_1 J (6 - b_2 N_{total}) \right) \Delta_1(t) + J \left( 8 J + b_1 (2 + b_2 N_{total}) \right) \Delta_2(t)}{2 (b_1 + 4 J)}$$

$$\frac{d \Delta_2(t)}{dt} = - \frac{J \left( 8 J + b_1 (2 + b_2 N_{total}) \right) \Delta_1(t) + \left( b_1^2 + 8 J^2 + b_1 J (6 - b_2 N_{total}) \right) \Delta_2(t)}{2 (b_1 + 4 J)}$$
This set of coupled differential equations is of the form:

\[
\frac{d\vec{\Delta}}{dt} = M\vec{\Delta} \quad \text{where} \quad M = \begin{pmatrix} a & b \\ b & a \end{pmatrix}
\]

\[a = -\left(\frac{b_1^2 + 8J^2 + b_1J(6 - b_2N_{\text{total}})}{2(b_1 + 4J)}\right) \quad \text{and} \quad b = -\left(\frac{J(8J + b_1(2 + b_2N_{\text{total}}))}{2(b_1 + 4J)}\right).
\]

The eigenvectors of this system are \(\begin{pmatrix} 1 \\ 1 \end{pmatrix}\), when \(\Delta_1 = \Delta_2\) and \(\begin{pmatrix} 1 \\ -1 \end{pmatrix}\), when \(\Delta_1 = -\Delta_2\). The corresponding eigenvalues are \(\lambda_1 = (a + b)\) and \(\lambda_2 = (a - b)\), which are equal to:

\[\lambda_1 = -\frac{b_1}{2} - 2J \quad \lambda_2 = b_1\left(-\frac{1}{2} + \frac{b_2JN_{\text{total}}}{b_1 + 4J}\right)\]

The eigenvalue \(\lambda_1\) is always negative, so perturbations along the \(\begin{pmatrix} 1 \\ 1 \end{pmatrix}\) eigenvector decay exponentially back to the fixed point for all parameter values. On the other hand, \(\lambda_2\) can be negative or positive. When this eigenvalue is positive, perturbations along the \(\begin{pmatrix} 1 \\ -1 \end{pmatrix}\) eigenvector grow exponentially, breaking symmetry. The \(\lambda_2\) eigenvector switches from negative to positive at the following critical value of \(b_2\):

\[b_2 = \frac{b_1 + 4J}{2JN_{\text{total}}}.
\]

When \(b_2\) is smaller than this value, the fixed point is a stable equilibrium, and the system maintains deadlocks. When \(b_2\) is larger than this value, the fixed point is an unstable saddle point; small perturbations grow exponentially, allowing for deadlock-breaking.
Appendix 4-2: Persistence effects at different group sizes. Effect of persistence (inverse of maximum giving-up rate constant) on maximum coordination for small, moderate, and large groups. Maximum giving-up rate constant is the maximum possible as defined by the function, actual values will depend on the number of individuals in each group. Extent of coordination is defined as the difference in the number of individuals pulling right and left, divided by the total number in the system. Maximum coordination is the maximum observed over a given time period, rather than an absolute maximum; higher values on the y-axis indicate faster convergence. Top row: uninformed rules, middle row: oblivious rules, bottom row: informed rules. Left column: total group size = 6, middle column: total group size = 20, right column: total group size = 200. Lines with smaller dashes indicate lower directional bias.
Appendix 4-3: Persistence and sensitivity effects in informed case at different group sizes.
Effect of persistence (inverse of maximum giving-up rate constant) on maximum coordination in small, moderate, and large informed groups at low (gradual) shape values. Maximum giving-up rate constant is the maximum possible as defined by the function, actual values will depend on the number of individuals in each group. Extent of coordination is defined as the difference in the number of individuals pulling right and left, divided by the total number in the system. Maximum coordination is the maximum observed over a given time period, rather than an absolute maximum; higher values on the y-axis indicate faster convergence. Top row: shape parameter, $b_2 = 0.5$, which corresponds to the solid line in fig. 2C. Bottom row: $b_2 = 1$, which is less gradual. Left column: total group size = 6, middle column: total group size = 20, right column: total group size = 200.
### Appendix 5-1: P-values for post-hoc comparisons among species.

<table>
<thead>
<tr>
<th>Species pair</th>
<th>Individual persistence measurements</th>
<th>Group coordination</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Engagement time (Tukey’s p-value)</td>
<td>Directional fidelity (Tukey’s p-value)</td>
</tr>
<tr>
<td>F. pallidefulva &amp; F. obscuripes</td>
<td>0.051</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>F. podzolica &amp; F. obscuripes</td>
<td>0.012</td>
<td>0.31</td>
</tr>
<tr>
<td>P. longicornis &amp; F. obscuripes</td>
<td>&lt; 0.0001</td>
<td>0.025</td>
</tr>
<tr>
<td>F. podzolica &amp; F. pallidefulva</td>
<td>&lt; 0.0001</td>
<td>0.0026</td>
</tr>
<tr>
<td>P. longicornis &amp; F. pallidefulva</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>P. longicornis &amp; F. podzolica</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>
**Appendix 6-1: Results of model selection for speeds.**

<table>
<thead>
<tr>
<th>Predictors</th>
<th>ΔAIC</th>
</tr>
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<tbody>
<tr>
<td>Full model: Which.Obstacle + In.Obstacle? + Interaction + Random effect of trial nested within colony</td>
<td>16.4</td>
</tr>
<tr>
<td>Which.Obstacle + In.Obstacle? + Random effect of trial nested within colony</td>
<td>6.43</td>
</tr>
<tr>
<td>Which.Obstacle + Random effect of trial nested within colony</td>
<td>367</td>
</tr>
<tr>
<td><strong>In.Obstacle? + Random effect of trial nested within colony</strong></td>
<td><strong>0</strong></td>
</tr>
<tr>
<td>Random effect of trial nested within colony only</td>
<td>362</td>
</tr>
</tbody>
</table>
Appendix 6-2: Details of best-fit model for speeds. All coefficients are reported for square-root-transformed data.

<table>
<thead>
<tr>
<th></th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.662</td>
</tr>
<tr>
<td>Random effects on intercept</td>
<td></td>
</tr>
<tr>
<td>Variance among colonies</td>
<td>0.018</td>
</tr>
<tr>
<td>Variance within trials</td>
<td>0.011</td>
</tr>
<tr>
<td>Fixed effect</td>
<td></td>
</tr>
<tr>
<td>In.Obstacle?Yes</td>
<td>-0.065</td>
</tr>
<tr>
<td>(Coefficient acts on speeds while navigating obstacle)</td>
<td></td>
</tr>
</tbody>
</table>
Appendix 6-3: Details of model results for Bayesian analysis of backward runs. Posterior means are shown and 95% credible intervals in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Wall</th>
<th>Cul-de-sac</th>
<th>Trap</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \beta )</td>
<td>0.0019 (-0.15 – 0.15)</td>
<td>0.14 (0.07 – 0.20)</td>
<td>-0.22 (-0.26 – -0.19)</td>
</tr>
<tr>
<td>( \alpha_i ) mean</td>
<td>-0.39 (-0.64 – -0.14)</td>
<td>-0.58 (-0.74 – -0.42)</td>
<td>-0.58 (-0.72 – -0.44)</td>
</tr>
<tr>
<td>( \alpha_i ) standard deviation</td>
<td>0.42 (0.25 – 0.65)</td>
<td>0.27 (0.16 – 0.44)</td>
<td>0.29 (0.20 – 0.42)</td>
</tr>
<tr>
<td>( \theta ) (scale parameter)</td>
<td>36 (28 – 44)</td>
<td>11 (9.7 – 12)</td>
<td>33 (31 – 36)</td>
</tr>
</tbody>
</table>
Appendix 6-4: Response of individual ant paths to obstacles over time. Obstacles were placed in the path of ants returning from sugar water baits. Shown here are the proportions of ants forced to navigate the obstacle because they failed to avoid it, measured in 10 second increments every two minutes. The “Cul-de-sac 2” trial had low traffic for the first several minutes; the two points marked with red asterisks each represent just 1 ant hitting the obstacle and 1 ant avoiding. The other data points in the Cul-de-sac 2 trial were based on an average of 15.7 ants per data point, while there were an average of 10.7 ants and 8.5 ants per data point, respectively, for the Wall trial and Cul-de-sac 1. Vertical lines show the median and maximum lengths of time obstacles were in place during trials for our main experiments. Our trials did not last long enough to be substantially affected by avoidance cues.
Appendix 6-5: Trajectories of groups of ants navigating the wall for all trials (n = 22).
Warmer colors indicate earlier in time, cooler colors indicate later in the navigation process.
Appendix 6-6: Trajectories of groups of ants navigating the cul-de-sac for all trials (n = 19). Warmer colors indicate earlier in time, cooler colors indicate later in the navigation process.
Appendix 6-7: Trajectories of groups of ants navigating the trap for all trials (n = 20). Warmer colors indicate earlier in time, cooler colors indicate later in the navigation process.
Appendix 6-8: Proportions of time stalled in each trial while navigating the obstacle (left panel) and while unencumbered (right panel). Groups spend approximately equal proportions of time stalled regardless of whether they are obstructed or not. Proportions of time stalled do not substantially differ among colonies. LA and LD are colonies at Arizona State University, LM and LS are colonies at Biosphere 2.
Appendix 6-9: Mean speeds for groups navigating an obstacle (gray boxes) and while unobstructed (open boxes) for each trial. A: trials with the wall; B: trials with the cul-de-sac. Boxes include 50% of the data (going from the 25th to 75th percentiles), and whiskers extend to the lowest and highest values that are within 150% of the interquartile range. Dots are points outside that range. The best general linear model of speeds, determined using AIC, included whether the group was obstructed ($\beta = -0.065$) and a random effect of trial nested within colony. While speeds were reduced during obstacle navigation, the reduction in speed was only 10% on average, and amounted to a small change compared with the variation in speeds across trials.
Appendix 6-10: Densities of backward run distances of groups navigating obstacles at different time intervals. A: the wall; B: the cul-de-sac; and C: the trap. Each time interval is 67 seconds long (one-tenth the total time across all trials). Warmer colors indicate earlier time intervals, and cooler colors are later time intervals. Modeled in a Bayesian framework as a gamma distribution with a changing shape parameter, our estimate of the effect of time, $\beta$, in the cul-de-sac (B), is 0.13 (95% CI: 0.07 – 0.20). Thus, in the cul-de-sac, groups move further away from the nest the longer they have been navigating. We did not find strong evidence for this effect in the wall (A; $\beta = 0.0019$, 95% CI: -0.15 – -0.15), and found the opposite effect in the trap (C; $\beta = -0.22$, 95% CI: -0.26 – -0.19). The distribution of distances of backwards runs becomes more right-skewed over time in the cul-de-sac but not the other obstacles.
Appendix 6-11: Speeds of groups at different group sizes. Group sizes are jittered. Speed is positively correlated with group size, and this effect is consistent across colonies (Kendall’s $\tau = 0.44$, $P < 0.0001$).
Appendix 6-12: Neither sinuosity nor number of direction changes are not correlated with the mean number of ants (group size). A and B: Sinuosity in the wall (Pearson’s $r = -0.18$, $P = 0.43$) and cul-de-sac (Pearson’s $r = 0.25$, $P = 0.30$), respectively. C and D: Number of direction changes in the wall (Kendall’s $\tau = -0.19$, $P = 0.25$) and the cul-de-sac (Kendall’s $\tau = 0.17$, $P = 0.36$), respectively. Blue dots are points for colonies at Arizona State University (light blue: colony LA; dark blue: colony LD) and green dots indicate colonies at Biosphere 2 (light green: colony LM; dark green: colony LS).
Appendix 6-13: Group sizes over time of groups navigating the cul-de-sac (A) and in the trap (B). Group size reduced in the trap dramatically, as individuals spent less time grasping the object. Groups in the cul-de-sac maintain relatively constant group sizes. Light grey, unsmoothed lines (background) show raw speed data. Grey, smooth lines show the smoothed speed for each trial and black lines show smoothed speed across trials, all computed with LOESS.