REVIEW ARTICLE

# Cooperative transport in ants: a review of proximate mechanisms

H. F. McCreery · M. D. Breed

**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.

**Keywords** Cooperative transport · Group retrieval · Formicidae · Cooperative foraging · Behavioral rules · Recruitment · Persistence

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## 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: Czaczkes and Ratnieks, 2013; Berman et al., 2011). 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 alignment of workers' travel directions so that they exert forces in approximately the same direction. 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 alignment 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 (Czaczkes and Ratnieks, 2013; Berman et al., 2011; Moffett, 2010). 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 (Czaczkes and Ratnieks, 2013; Berman et al., 2011). 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.

## 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 et al., 2001; Franks, 1986; 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.

## Phases of transport

Figure 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 Fig. 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 quickly align movement directions (organization phase).
4. Together, the accumulated workers move the item—without dissection—toward the nest (transport phase).

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
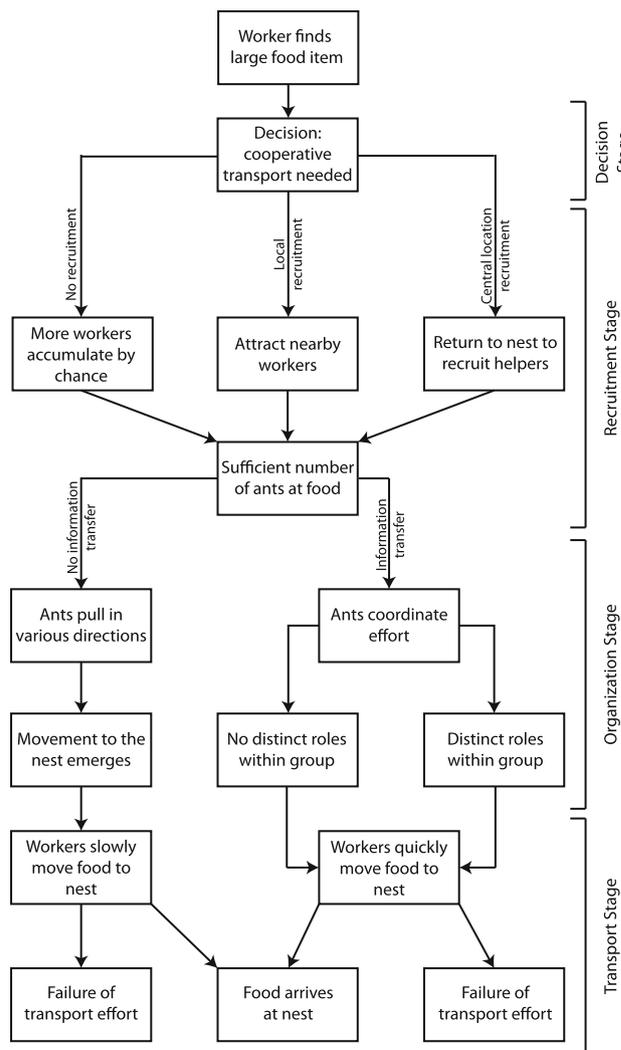


**Fig. 1** Generalized process of cooperative transport. Corresponding phases as described in text shown on the right. The distinction between the two paths of the flowchart corresponding to "Information transfer" and "No information transfer" is likely a gradient

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 (Cerdá et al., 2009; Cogni and Oliveira, 2004; Detrain and Deneubourg, 1997). For *Pheidole pallidula*, a load's resistance to movement affects the decision to engage in cooperative transport (Detrain and Deneubourg, 1997). *Pheidole 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-Schveitzer 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-Schveitzer et al., 2007). Once the prey is immobilized, these hunters can recruit other workers (non-hunters) to help with the transport. Daly-Schveitzer et al. (2007) observed recruitment behavior for various prey types. Prey that were <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-Schveitzer 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-Schveitzer 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 1 m 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 remarks the chemical trail back to the prey item. The recruited nest-mates follow her, though not immediately (Daly-Schveitzer et al., 2007). Similar recruitment behavior is observed in *F. 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-Schveitzer et al., 2007). Daly-Schveitzer 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-Schveitzer 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 and Ratnieks, 2012). 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 quickly (in 5–7 min) and can be followed with high accuracy (Czaczkes et al., 2013; Czaczkes and Ratnieks, 2012). In *P. oxyops*, these short-lived trails only last long enough for a worker recruited from the nest to reach a food item within 4 m (Czaczkes and Ratnieks, 2012). 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., 2013; Czaczkes and Ratnieks, 2012). 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 (Moffett, 1986). 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 (Berman et al., 2011; Moffett, 1992). 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 (Czaczkes and Ratnieks, 2013; Berman et al., 2011). 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 (but extra workers may defend prey, see 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 (reviewed in 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 *E. 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 *F. 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. *Eciton 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 (*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 *P. 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-Schveitzer 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-Schveitzer 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 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.

## 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 useful in a range of contexts, the total mass of objects carried cooperatively and individually
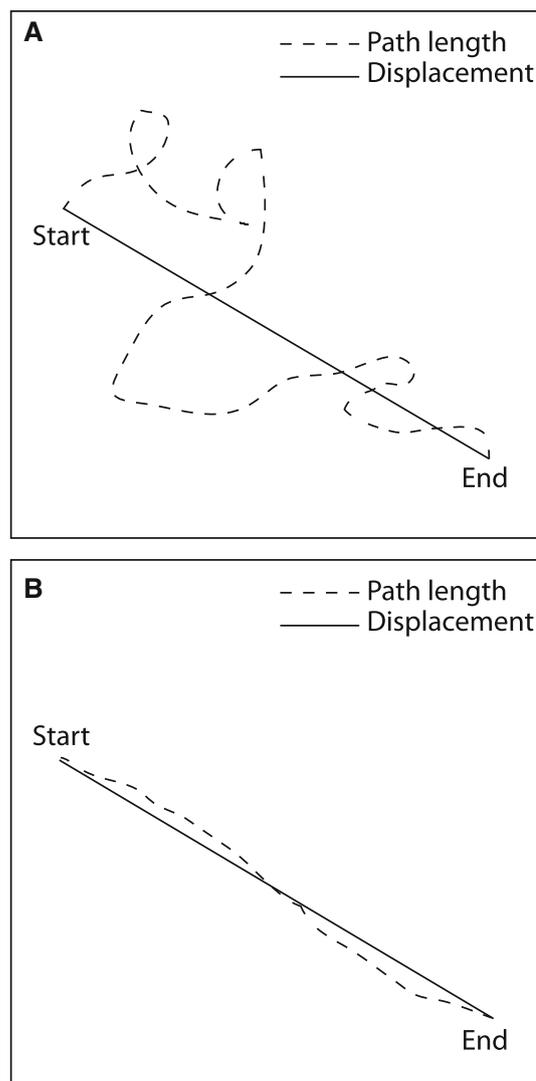


**Fig. 2** Sinuosity is defined as the total path-length (*dashed line*) divided by the shortest possible path (displacement; *solid line*). **a** Path with high sinuosity. **b** Path with low sinuosity

must be equal. For example, one might compare the efficiency of cooperatively transporting a 1 g cricket whole with efficiency of individually transporting a 1 g cricket that has been dissected into 20 pieces.

$$\text{Efficiency ratio} = \frac{\text{mean} (R_{\text{cooperative}})}{\text{mean} (R_{\text{individual}})}$$

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 >1, 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 <1, 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 <1 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, Fig. 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.

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.

## 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; Seeley and Visscher, 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 (Seeley and Visscher, 2003, 2004; Pratt et al., 2002; 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 five workers in a transport group, three 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 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 Fig. 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. Low mean 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 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 or 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.

## 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-Schveitzer 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. (2006) provide 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.

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