

Cooperative transport in ants (Hymenoptera: Formicidae) and elsewhere

Tomer J. CZACZKES & Francis L.W. RATNIEKS



Abstract

Cooperative transport, defined as multiple individuals simultaneously moving an object, has arisen many times in ants, but is otherwise extremely rare in animals. Here we review the surprisingly sparse literature available on cooperative transport. Cooperative transport abilities in ants are a continuum, but three general syndromes are described: uncoordinated transport, in which transport is slow, poorly coordinated and characterised by frequent and long deadlocks; encircling coordinated transport, in which transport is fast, well coordinated, and with few deadlocks; and forward-facing coordinated transport, carried out exclusively by army ants, in which one worker, usually of larger size, straddles an item at the front while one or more smaller workers help to lift at the back. In the two coordinated syndromes, the groups of ants involved constitute teams, and specialised recruitment to large items and adjustment of carrier number to match item size may occur. Some features of cooperative transport are specific adaptations, whilst others are already present in the behaviour of ants carrying items alone. One major benefit of cooperative transport appears to be that it allows a colony to utilize large food items in an environment with aggressive or dominant competitors by quickly removing the item to the nest rather than having to cut it up or consume it on the spot. In addition, compared to individual transport, cooperative transport may have other benefits such as increased transport speed or efficiency.

The study of cooperative transport also includes computer simulations and robots. These provide biologists with new perspectives and also formalise questions for further study. Likewise, lessons learned from cooperative transport in ants can inform computer scientists and roboticists.

Key words: Cooperative transport, organisation, foraging, group retrieval, ants, review, teams.

Myrmecol. News 18: 1-11 (online 24 October 2012)
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 19 April 2012; revision received 20 June 2012; accepted 28 June 2012
Subject Editor: Alexander S. Mikheyev

Tomer J. Czaczkcs (contact author) & Francis L.W. Ratnieks, Laboratory of Apiculture & Social Insects, School of Life Sciences, University of Sussex, Falmer, United Kingdom BN19QG. E-mail: tomer.czaczkcs@gmail.com

Introduction

Over the last hundred years the range of abilities considered to be uniquely human has diminished. For example, a sense of fairness or an aversion to inequality has been demonstrated in both monkeys (BROSNAN & DE WAAL 2003) and dogs (RANGE & al. 2009). Tool use, another attribute once considered uniquely human, is now known in many taxa (e.g., chimpanzees, GOODALL 1964; crows, HUNT 1996; fish, PAŠKO 2010; octopuses, FINN & al. 2009; and even insects such as ants, BANSCHBACH & al. 2006; and solitary wasps, BROCKMANN 1985). However, one behaviour that is almost exclusively confined to humans is cooperative transport. Unlike tool use, our closest relatives the great apes rarely seem to do this. Apart from humans, the only animals that regularly perform large scale cooperative transport are ants. Cooperative transport can be defined as two or more individuals simultaneously moving an item from one location to another. Although cooperative transport is a widely known behaviour of ants, and often features in cartoons and the popular image of ants, it is surprisingly understudied and what information exists has never been comprehensively reviewed in the published literature, although MOFFETT (1987) surveys cooperative transport in his PhD thesis and later in MOFFETT (2010). Here

we address this deficiency by collating what is known about cooperative transport in ants. In doing this we also discuss whether specific adaptations are used or required for cooperative transport, the ecology of cooperative transport, and also introduce a simple terminology for the different syndromes of cooperative transport observed. Lastly, we examine cooperative transport outside humans and ants including research on cooperative transport in other animals, robots and via computer simulations.

Syndromes of cooperative transport in ants

Cooperative transport, also referred to as group retrieval, group transport or cooperative carrying, is common but far from universal in ants. It is known in at least 40 genera in different subfamilies of the Formicidae (HÖLLDOBLER & WILSON 1990, MOFFETT 1992, MOFFETT 2010). Although no formal comparative analysis has been carried out, this strongly suggests that cooperative transport has evolved multiple times in ants. There is also much variation in apparent sophistication and effectiveness. The cooperative transport abilities of particular ant species lie on a continuum from never occurring to highly specialised, efficient and rapid. For convenience, we categorize cooperative transport

Box 1: Different definitions of "teams". Definitions range from the highly restrictive necessity for different castes, to the highly inclusive definition used in daily parlance. The highly restrictive definition includes very few natural examples, limited only to new and old-world army ants. The highly inclusive definition encompasses all cooperating groups, and so is perhaps too uninformative for scientific discourse.

Name / proponent	Description	Requires	Examples from sports
Different castes working concurrently (HÖLLDOBLER & WILSON 1990)	"teams ... can be defined as members of different castes that come together for highly coordinated activity in the performance of a particular task"	<ul style="list-style-type: none"> • Multiple individuals working towards the same goal • concurrently performed subtasks • members in non-interchangeable roles 	American Football, Rugby. Different non-interchangeable "castes" (fast runners, e.g., wingers in rugby, large tacklers, e.g., props in rugby) work concurrently, performing different subtasks (wingers receive passes and score tries, props tackle opposing teammates)
Different sub-tasks being performed concurrently (ANDERSON & FRANKS 2001)	"A team task requires different subtasks to be performed concurrently for successful completion." A team is a group of individuals performing a team task. Individuals not only have to work concurrently, they must also coordinate their different contributions.	<ul style="list-style-type: none"> • Multiple individuals working towards the same goal • concurrently performed subtasks 	Basketball, Polo. Different subtasks (e.g., shoot guard or centre in Basketball) performed concurrently, but no extreme physical differentiation of players.
Daily parlance (MOFFETT 2010)	Any group of individuals that work towards a single goal. Synonymous with "cooperating group".	<ul style="list-style-type: none"> • Multiple individuals working towards the same goal 	Tug-of-war, Bowling, Relay running. In a tug-of-war players perform identical tasks concurrently. In bowling and relay running players perform identical roles, and do so singly.

in ants into three general syndromes: uncoordinated transport, encircling coordinated transport, and forward-facing coordinated transport.

In uncoordinated transport, item movement is characterised by frequent deadlocks in which ants pull in opposite directions resulting in no forward motion (SUDD 1965, MOFFETT 1986, PRATT 1989, MOFFETT 1992). These deadlocks are resolved by random changes in the composition, orientation or behaviour of the group members, which indicates lack of coordination (SUDD 1965). SUDD (1965), in an extensive study of cooperative prey transport by *Myrmica rubra* (LINNAEUS, 1758) and *Formica lugubris* ZETTERSTEDT, 1838, both of which perform uncoordinated transport, found three discrete stages to transport. Transport begins when the first ants find the food item (stage one), but then stops as more ants find the item and deadlock occurs (stage two). Deadlock can last up to ten minutes, until random changes cause the deadlock to end. The third stage is characterised by higher speed and path straightness than the first and second stages, implying better organisation of the carriers who have by chance brought themselves into an effective alignment. However, no evidence was found of specific cooperative behaviour: Ants did not synchronise their pulling efforts and often pulled in opposite directions. A burst of motion occurred when ants by chance attempted to pull the item in the same direction. Whilst the ants "agreed" about the general direction the item is to be moved in, they "disagreed" on how to achieve this. Nonetheless, ants did not assemble randomly around the food item, but over time came to be more evenly spaced around the item. Eventually, the groups of ants could also exert larger forces than individual ants could alone. Thus, whilst uncoordinated, this syndrome of cooperative transport can be useful for dislodging snagged items or for slowly retrieving items too large for a single ant.



Fig. 1: *Carebara simalurensis* cooperatively transporting a large brood item. Notice how the ants lift the item using the underside of their heads and front legs. A similar behaviour is displayed by *Pheidologeton diversus*. In contrast, ants carrying items individually grasp with their mandibles, as shown by the ant on the right which is transporting a small brood item. Image copyright Mark W. Moffett / Minden Pictures.

In the second syndrome, encircling coordinated transport, ants are recruited to a food item, encircle it, and quickly transport the item back to the nest once a sufficient number of ants have assembled to move the item (e.g., *Pheidologeton diversus* (JERDON, 1851), M. Moffett, pers. comm.; *Leptogenys diminuta* (SMITH, 1857), MASCHWITZ & STEGHAUS-KOVAC 1991; *Pheidole oxyops* FOREL, 1908, see CZACZKES & al. 2010; *Pheidole pallidula* (NYLANDER, 1849), TOFFIN 2003; *Aphaenogaster cockerelli* ANDRÉ, 1893, see HÖLLDOBLER & al. 1978, BERMAN & al. 2011; *Paratrechina longicornis* (LATREILLE, 1802), T. Czaczkes, unpubl.). Deadlocks are not a conspicuous feature, except briefly if the item becomes snagged along the route. During encircling cooperative transport, ants at the front of the

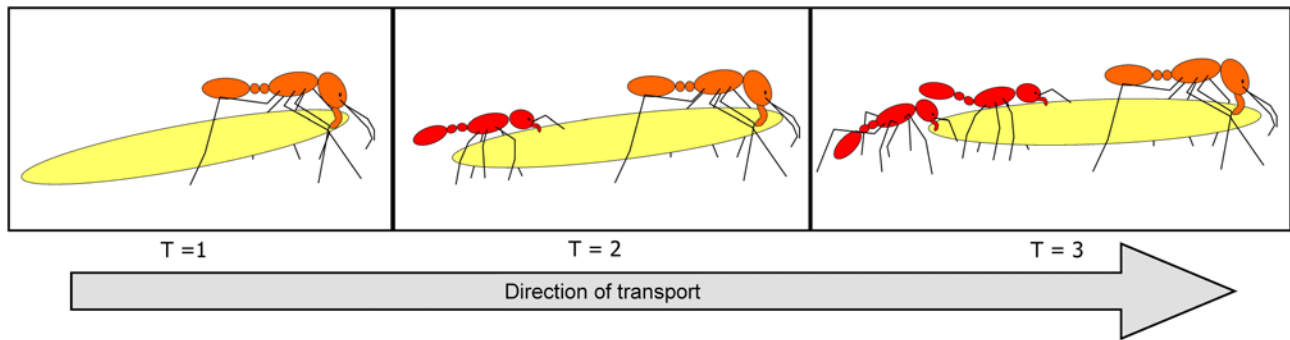


Fig. 2: Forward-facing cooperative transport. At $T = 1$ a larger worker begins to lift and drag the item forward, but due to the weight of the item, and drag and rotational forces, transport is slow. At $T = 2$ a smaller worker, sensing a slow-moving item, joins behind the larger worker and assists in lifting, thereby reducing rotational forces and drag, and allowing the item to move faster. If the item is still moving below a threshold transport speed another smaller worker might join in $T = 3$ and assist in transport.

item lift and pull or drag the item whilst walking backwards, ants at the back of the item lift the item and walk forwards, and ants at the sides lift or drag and walk sideways. These are distinct subtasks (*sensu* ANDERSON & FRANKS 2001) which must be carried out concurrently, and thus the ants engaged in encircling cooperative transport constitute a team (ANDERSON & FRANKS 2001). See Box 1 for a further discussion of the various definitions of teams.

Individual scouts assess the need for cooperative transport by first trying to move an item, and if the item cannot be moved recruitment is initiated by the scout (HÖLDOBLER & al. 1978, TRANIELLO 1983, DETRAIN & DE-NEUBOURG 1997, DALY-SCHWEITZER & al. 2007). The number of ants transporting the item is often adjusted to the size of the item (TRANIELLO 1983, TRANIELLO & BESH-ERS 1991, ROBSON & TRANIELLO 1998), although this is not mediated by the discoverer's recruitment behaviour. Numbers of transporting ants can be reduced by ants leaving the item, and can be increased if the item is not being moved or is not moved rapidly as this results in transporting ants leaving the item and initiating further recruitment (ROBSON & TRANIELLO 1998). The availability of space around the perimeter of the item also limits the number of transporting ants (MOFFETT 1988). Having more carriers around an item results in higher transport speeds, up to a point (MOFFETT 1988, CERDÁ & al. 2009, T. Czaczkes, unpubl.).

Food items are the primary targets of cooperative transport. In species which perform coordinated transport, large proportions of a colony's food by mass can be retrieved via cooperative transport (e.g., 72% in *Aphaenogaster senilis* MAYR, 1853, see CERDÁ & al. 1998; 85% in *Lasius niger* EMERY, 1893, see TRANIELLO 1983; 78% in *Pheidole oxyops*, see CZACZKES & al. 2010). Other cooperatively transported items include stones removed during nest excavation and large waste items such as beetle carapaces (T. Czaczkes, unpubl. in *P. oxyops*), large soil particles to be used in nest construction (MOFFETT 1987) and enslaved *Myrmecocystus* honey pot ant repletes (HÖLDOBLER 1981). Large brood items are also moved cooperatively, and MOFFETT (1992) suggests that this may be the original purpose for which cooperative transport evolved, given that even ant species that show no group transport of food have brood items much larger than workers, such as the pupae of queen

ants, that they need to be able to move rapidly during colony emergencies (see Fig. 1).

In the third syndrome, forward-facing cooperative transport, one ant lifts and carries the item from the front whilst facing forwards, and one or more other ants join along the item in a line also facing forward (FRANKS 1986, FRANKS & al. 2001) (see Fig. 2). Forward-facing cooperative transport has been described only in army ants, but in three genera on three continents: the Neotropical *Eciton* army ants (FRANKS 1986), the African driver ant species *Dorylus wilverthi* EMERY, 1899 (FRANKS & al. 1999), and the Asian *Leptogenys borneensis* (WHEELER, 1919) (C. Von Beern, unpubl., see Appendix, as digital supplementary material to this article, on the journal's web pages). Except in *L. borneensis*, which is monomorphic, carrying groups are frequently composed of a larger ant straddling and lifting the item from the front and one or more smaller ants, which also straddle and lift the item, from the middle or rear. Transport begins with the single front carrier. Other ants then join the group, assisting by lifting and carrying from behind, which reduces rotational forces and drag (FRANKS 1986). Additional ants may join the back of the item, increasing transport speed, until the transport speed approaches the normal marching speed of the column (FRANKS 1986) (see Fig. 2). Thus, matching of ant number to prey size also occurs in forward-facing coordinated transport (FRANKS 1986, FRANKS & al. 2001). In *Eciton* the front ants are often sub-majors, which have longer legs than medias but shorter mandibles than the majors, and are a specialised carrier or porter caste (FRANKS 1986). The groups of forward-facing carriers are also often described as a team (FRANKS 1986, FRANKS & al. 1999).

Adaptations and preadaptations to cooperative transport

Adaptations for cooperative transport: Early writers (GRASSÉ 1934, RABAUD 1937, CHAUVIN 1950) concluded that during cooperative transport the transporting ants behave identically to individual ants, taking no notice of the actions of the other ants. Indeed, SUDD (1965) concluded after his study of cooperative transport in *Pheidole crassinoda* EMERY, 1895 that "the behaviour of individuals in a transporting group appears to contain no element of behaviour that were not shown by single transporting ants". However, more recent results demonstrate that this is not

the case. In *Eciton burchelli* (WESTWOOD, 1842) there is not only a specialist porter caste for carrying large loads (POWELL & FRANKS 2005, POWELL & FRANKS 2006) but workers also possess behavioural rules that refine cooperative transport. For example, ants joining a team in which their strength is greater than that needed to move the item efficiently soon disengage from the item and leave the group (FRANKS & al. 2001). *Pheidologeton diversus* workers transport items individually by grasping with their mandibles, but during cooperative transport groups of ants lift the item by pushing against it with their front legs and head (MOFFETT 1988) (see Fig. 1). In *Formica schaufussii* MAYR, 1866 the scout ant which discovers a large food item and recruits nestmates maintains the cohesion of the recruited ants – if the scout ant is removed whilst leading the recruits to the food item, the group disbands and foraging is abandoned (ROBSON & TRANIELLO 2002).

Adaptations for cooperative transport outside carriage – the example of recruitment: Behaviours additional to the actual moving of the item may also be under selection as part of cooperative transport. One example of this is the recruitment of nestmates to an item. Recruitment specialised for cooperative transport is a good example of such an adaptation, and can be contrasted with well studied recruitment to aphid patches, and their laboratory equivalent: the sucrose syrup feeder. Many ants utilize semi-permanent replenishing food sources at specific locations, such as aphid patches. Naïve ants can be recruited to such food sources by pheromone trails, but as nestmate ants make repeated visits to the food source and the food source is long-lived, accurate trail pheromone following may not be essential. In addition, experienced ants can use route memories to relocate the feeding site (HARRISON & al. 1989, GRÜTER & al. 2011). Thus, in *Lasius niger* (LINNAEUS, 1758), a species that recruits mostly to aphid patches and does not perform cooperative transport, pheromone trails last for up to 20 hours (EVISON & al. 2008), but are followed with relatively low accuracy (62 - 70% accuracy at a T-bifurcation (GRÜTER & al. 2011)). By contrast, in cooperative transport recruitment is to a single point, which places a premium on accurate trail following. In *Pheidole oxyops*, which relies heavily on cooperative transport, 85% of recruits chose the correct branch at T-bifurcation on a fresh trail (CZACZKES & RATNIEKS 2013) laid by a single ant that discovered the food item, could not move it, and so laid a trail back to the nest. The need for accurate trail following, combined with the fact that a long-lived trail is not needed, has resulted in the convergent evolution of trail pheromones that evaporate rapidly, with complete decay of the item-discoverer's trail occurring in just 5 - 7 minutes (*Aphaenogaster albisetosus* MAYR, 1886, see HÖLDOBLER & al. 1978; *P. oxyops*, see CZACZKES & RATNIEKS 2013; *Paratrechina longicornis*, T. Czaczkes, unpubl.). In contrast, the trail of mass recruiting non-cooperatively transporting ants, may last much longer: up to 24 hours in *L. niger* (see EVISON & al. 2008), up to 48 hours in *Monomorium pharaonis* (LINNAEUS, 1758) (JACKSON & al. 2006). A short-lived trail pheromone may indeed be adaptive for cooperative transporters, as once items have been removed they do not replenish, and so continued recruitment to a location would serve no purpose and could even increase the exposure of workers to risks outside the nest. A short-lived trail and high accuracy may

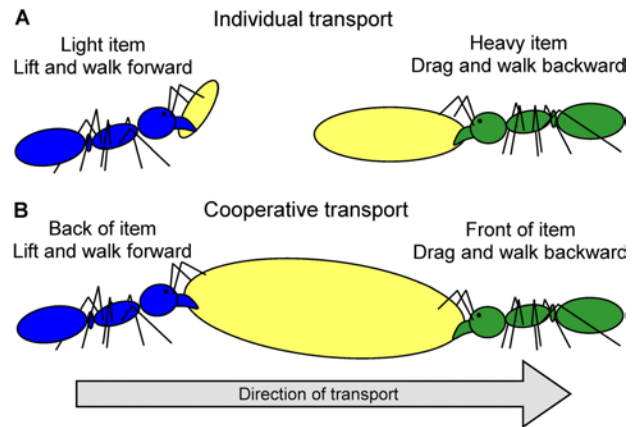


Fig. 3: One potential adaptation distinguishing coordinated from uncoordinated cooperative transport. During individual transport ants carrying light loads lift the item and walk forward. When transporting heavy loads individual ants walk backwards and drag. By relaxing the transition from lifting and walking forward to dragging backward when multiple ants are transporting an item, ants would be able to begin assisting in cooperative transport even when the item is being moved slowly enough to trigger a switch to walking backwards and dragging if the item was being individually transported.




also be an adaptation to cooperative hunting of large mobile prey (MASCHWITZ & STEGHAUS-KOVAC 1991, WITTE & al. 2010).

Ants which rely on cooperative transport must recruit sufficient workers to move a food item before other colonies of their own or other species, or indeed non-ant competitors, find the item (see next section). Thus, some ant species that use cooperative transport can decrease the time needed to recruit a transport team using local recruitment, either by emitting an air-born attractant pheromone (HÖLDOBLER & al. 1978, TRANIELLO 1983), or by workers intercepting a pheromone trail to the nest and following it towards the food item (CZACZKES & RATNIEKS 2012).

Distribution of ants around a transported item

The distribution of ants around a transported item is also far from random. Some species tend to carry items by the corners, which increases speed of transport (CZACZKES & al. 2010), and by the front and back, avoiding the side (SUDD 1965, CZACZKES & al. 2010). These non-random arrangements are driven by ants preferentially leaving unappealing grasping points (in this case, side sections of an item), and preferentially joining onto more appealing grasping points (in this case, corner sections) (CZACZKES & al. 2010). More ant-power is usually deployed at the front, and less at the back, as demonstrated during team transport by army ants (FRANKS & al. 1999). Where large-bodied worker castes are not available, multiple monomorphic ants can arrange themselves to produce this pattern by having more carriers at the front than the back (CZACZKES & al. 2010). The use of minors collectively as a "plastic supercaste" (FRANKS 1986) allows greater flexibility when foraging on unpredictable food sources (TRANIELLO 1989) given that worker demography cannot change rapidly according to short-term needs and that maintaining a standing supply of specialist castes is expensive (OSTER & WILSON 1978, BOURKE & FRANKS 1995).

Tab. 1: The three syndromes of cooperative transport.

Example species	General description	Example image
Uncoordinated cooperative transport		
<p><i>Myrmica rubra</i>, <i>Formica lugubris</i>, <i>F. rufa</i> LINNAEUS, 1761, <i>Daceton armigerum</i> (LATREILLE, 1802), <i>Ectatomma ruidum</i> (ROGER, 1860), <i>Anoplolepis longipes</i> (JERDON, 1851)</p> <p>See CHAUVIN (1950), SUDD (1965), MOFFETT (1992).</p>	<p>Slow transport with frequent, long lasting deadlocks. All ants attempt to drag the item towards the destination – ants at the back do not attempt to lift and walk forward.</p>	 <p>Uncoordinated transport in a <i>Formica</i> species. A deadlock has occurred during transport, with the ants on either side of the beetle pulling in opposite directions.</p>
Encircling coordinated transport		
<p><i>Pheidologeton diversus</i>, <i>Carebara pygmaea</i>, <i>Pheidole oxyops</i>, <i>P. pallidula</i>, <i>Aphaenogaster cockerelli</i>, <i>Paratrechina longicornis</i>, <i>Lasius neoniger</i>.</p> <p>See MOFFETT (1988), ROBSON & TRANIELLO (1998), CZACZKES & al. (2010).</p>	<p>Rapid transport with deadlocks mostly absent. Ants at the leading edge drag, ants at the back lift, push or carry. Large items retrieved cooperatively often make up a sizeable proportion of total retrieved biomass. Recruitment for cooperative transport is rapid. The need for recruitment is assessed by tractive resistance of the item.</p>	 <p>Left: <i>Pheidole oxyops</i> cooperatively transporting a stingless bee (<i>Melipona scutellaris</i>). Right: The Longhorn Crazy Ant <i>Paratrechina longicornis</i> cooperatively transporting royal brood (right).</p>
Forward-facing coordinated transport		
<p><i>Eciton burchelli</i>, <i>E. hamatum</i> (FABRICIUS, 1782), <i>Dorylus wilverthi</i>, <i>Leptogyne borneensis</i></p> <p>See FRANKS (1986), FRANKS & al. 2001).</p>	<p>Rapid transport with no deadlocks. All carrying ants face in the direction of carriage. A leading ant, usually large, straddles the item and lifts. Other ants, usually smaller, join behind the leading ant, also straddle the item, help lift and reduce rotation (see Fig. 1). Workers join until the item is moving at standard column walking speed.</p>	 <p><i>Eciton</i> army ants cooperatively transporting a centipede segment. Note the larger submajor with very long legs at the front. Image reproduced with permission of Ammonite (www.ammonite.co.uk)</p>

Adaptive behaviours that are not adaptations

Behaviours that make cooperative transport more efficient need not necessarily be adaptations for cooperative transport. As mentioned above, during cooperative transport (except team transport and the derived transport of *Pheidologeton* and *Carebara*) ants at the front walk backwards dragging the item, while ants at the back of the item walk forwards whilst lifting and carrying (Tab. 1) (MOFFETT 1992, CZACZKES & al. 2010). This might at first be considered an adaptation to cooperative transport, but may in fact simply be a behaviour carried over from individual transport. When ants transport an item individually they lift and carry light items facing forward, but drag heavy items whilst facing backwards (SUDD 1960). The same rules may be used during cooperative transport: if the item

is not in motion, or moving slowly, the item is grasped and dragged. If the item is moving rapidly, and thus is "easy" for a joining ant to move, the item is grasped and lifted (Fig. 3). As ants first join the front of the item, and only then begin to join the back (CZACZKES & al. 2010), these rules would result in efficient cooperation without any new adaptations to the cooperative situation. Likewise, groups of ants are capable of rotating an item so that it assumes a low drag orientation (CZACZKES & RATNIEKS 2011). This behaviour, whilst beneficial in that it reduces drag forces and so reduces energy expenditure, is probably not a specific adaptation to cooperative transport as it can arise from the same rules utilised by an individual forager (see Fig. 4): On encountering a large item, ants attempt to drag it to the nest. This will cause the item to pivot around the point of highest drag, resulting in a reorientation. Some behaviours

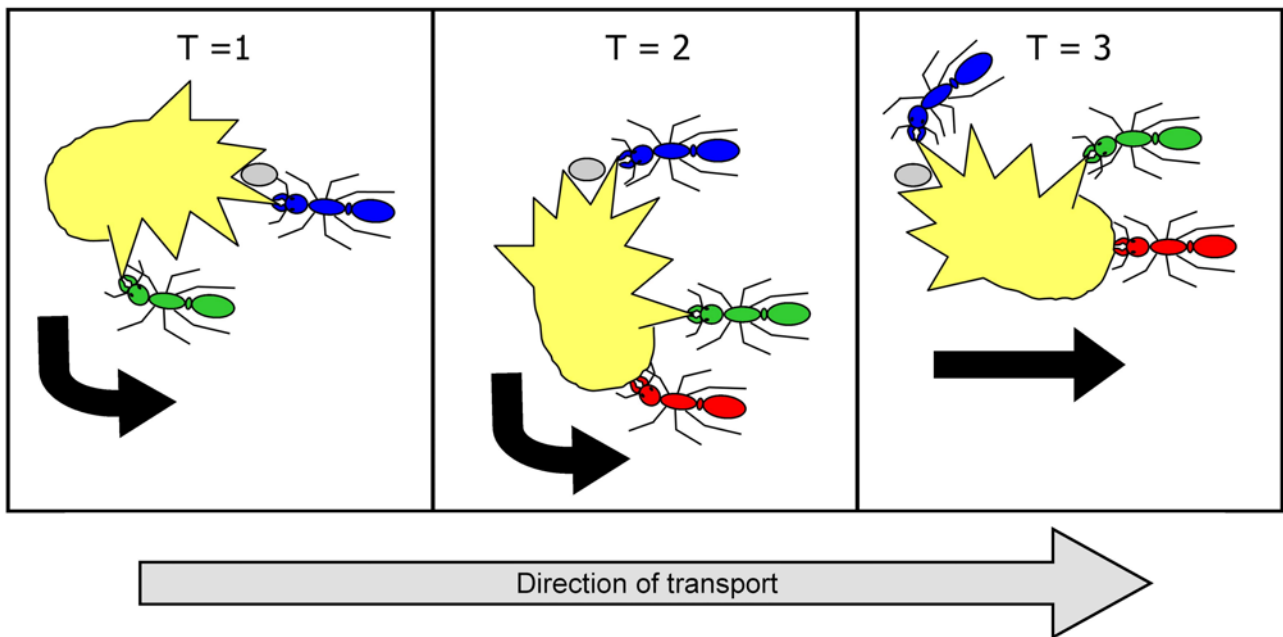


Fig. 4: The turning of a food item reduces drag and facilitates cooperative transport – an adaptive behaviour that is not an adaptation. Ants assemble around an item and attempt to move it in the direction of transport ($T = 1$). However, the item is snagged (small grey oval). The blue ant attempts to pull the item, to no avail. The green ant, by pulling the item, causes it to pivot around the point where it is caught. In $T = 2$ the item is still somewhat snagged, and the pulling of the blue and green ants cannot dislodge the item. However, the pulling of the red ant causes the item to pivot again. In $T = 3$ the item is in an orientation that reduces drag, and transport proceeds. Image based on CZACZKES & RATNIEKS (2011).

used by individual foragers are also useful during cooperative transport, and could be considered preadaptations which, while facilitating the emergence of cooperative transport, were not specifically evolved in a cooperative transport context.

What adaptations do coordinated transporters show during cooperative transport?

Perplexingly, distinguishing behavioural adaptations which allow coordinated cooperative transporters to be especially effective during transport has proven difficult. One possibility is that the willingness of ants to grasp items by the sides and walk sideways, a behaviour never observed for long during individual transport, is such an adaptation. Another possible adaptation is a relaxation of the switching between walking forward and lifting when carried items are light and dragging and walking backwards when items are heavy (Fig. 3). During coordinated cooperative transport, ants joining the back of an item assist by lifting and walking forward, even if the item is moving slower than their normal walking speed. During individual transport, when items are being moved too slowly, the ant switches from lifting and walking forward to dragging backwards (SUDD 1960). How individuals sense that an item is being cooperatively transported, so that this switch should not be made, is unknown. Lastly, the specialised carrying posture used by *Pheidologeton* and *Carebara* during cooperative transport (MOFFETT 1988 – see Fig. 1) is a clear adaptation to cooperative transport.

The ecology of cooperative transport – why do it?

Perhaps the most obvious benefit of cooperative transport is to retrieve items larger than cannot be retrieved by an in-

dividual worker. By transporting food items cooperatively, ants become in effect a larger organism (CARROLL & JANZEN 1973, CERDÁ & al. 1998, HÖLLDOBLER & WILSON 2009). However, many ant species that do not perform cooperative transport also forage on large food items. Why then is cooperative transport needed, and why do only some ant species use cooperative transport?

Ants that forage on large food items without cooperative transport either recruit en masse to the item and feed in situ, even in rare cases bringing brood to the item to feed (MASUKO 1990), or dissect the item and carry parts back individually (DJIÉTO-LORDON & al. 2001, RICHARD & al. 2001, YAMAMOTO & al. 2009). Large food items will eventually have to be dissected in order to be consumed, and so we must ask why it is preferential to dissect items in the nest rather than in situ. Once sufficient individuals reach the prey item it is effectively dominated, and unavailable to competitors (HÖLLDOBLER & al. 1978, ADAMS & TRANIELLO 1981, TRANIELLO 1983). However, dissection can take several hours (YAMAMOTO & al. 2009), leading to the risk that the item will be discovered and dominated by superior competitors. Cooperative transport is important for ants which cannot win direct competition, as it assists them in scramble competitions by allowing rapid retrieval of the item before larger ants can remove the food item, or ants with large colonies can recruit *en masse* to the item (HÖLLDOBLER & al. 1978, TRANIELLO 1983, 1987, TRANIELLO & BESHES 1991). Cooperative transporters mostly retrieve medium or large items, but very large items are not transported as these cannot be moved swiftly enough and so would often be lost to competitors (CERDÁ & al. 1998). However, these arguments do not fit the army ant situation as well, given that army ants perform cooperative transport

even though they face little competition and also dissect prey items in situ. We suggest that in army ants cooperative transport is not specifically for removing items more rapidly to avoid competition, but to allow carriers to keep up with the dense flow of traffic and so reduce the possibility of traffic jams. As army ants often raid over long distances with extended trails (SCHNEIERLA 1933), reducing time and energetic costs may be significant (see below). Whilst useful for avoiding competition and increasing retrieval speed in ground foraging species, cooperative transport is very rare in arboreal species. Cooperative transport on branches is risky, as cooperatively transporting groups are more likely to fall off branches than individuals (YAMAMOTO & al. 2009).

Cooperative transport may also provide energetic benefits. In some, but not all, cooperatively transporting species cooperative transport has been found to be super-efficient (HÖLDOBLER & al. 1978, FRANKS 1986, MOFFETT 1988, FRANKS & al. 1999). That is, the loads transported by a group could not be transported as rapidly (or in some cases at all) by the same ants individually, no matter how the item was fragmented. For example, two cooperating workers might be able to carry three times the load weight that a single worker could. This increase in efficiency might result from a reduction in drag as the item is lifted, or from a reduction in rotational forces, or both. As a similar number of ants are required to dissect the item in situ or in the nest, transporting the item to the nest may result in less ants having to be recruited and having to travel to the item.

Transporting food items back to the nest may act as a form of task partitioning, making use of idle nest-based workers by allocating the task of dissection to nest workers whilst foragers can return to foraging or other tasks (MOFFETT 1987). Even more effective task partitioning resulting from retrieval of large food items is the "dissection" and consumption of food items by brood, which cannot do any other task. Similarly, the time-consuming task of dissection can be delayed by bringing food to the safety of the nest, where dissection can take place once foraging is over.

Lastly, cooperative transport may be used when fragmentation is not an option. Ants may use cooperative transport to remove tough waste material, such as stones or beetle carapaces, from the nest (T. Czaczkes, unpubl.). MOFFETT (1992) has also suggested that cooperative transport may be widespread when transporting royal brood, which can be large and is obviously non-divisible. He gives the example of *Carebara simalurensis* (FOREL, 1915) (Fig. 2), which transports brood using a highly derived coordinated transport (i.e., using the specialised behaviour of carrying by lifting with the head and forelegs), but does not cooperatively transport food items (MOFFETT 1992).

Cooperative transport elsewhere in nature

Cooperative transport is frequent in both ants and humans. Although it is not their exclusive domain, there are very few reports or anecdotal accounts of cooperative transport in other animals. Social spiders (*Anelosimus eximius* KEYSERLING, 1884) have been reported to cooperatively move prey items from the outskirts of their communal web towards the centre (VAKANAS & KRAFFT 2004). The spiders weave and then tension a strand of "traction silk" between the web and the prey. The prey is then cut free of the web, causing it to move in the direction of the traction silk. On one

occasion, one spider cut the web, one pulled the prey, a third pushed, and a fourth lifted the prey item to prevent it getting stuck on the web. This seemingly advanced team transport is, however, extremely slow (about 1 cm / min) and occurs over very short distances (about 10 cm in total) within what is effectively the nest. There seem to be no specific recruitment behaviour signals. Spiders are attracted via vibrations in the web caused by the prey and perhaps by other spiders.

In some dung beetles, such as *Canthon cyanellus* (LECONTE, 1859), males and females cooperate in rolling a dung ball (FABRE 1911, HALFFTER 1997). Females may be attracted by a solitary male rolling a dung-ball, although males will also recruit females using long-range pheromone signals even if rolling has already been completed before a female is attracted. The organisation of the pair is non-random, with the male occupying the energetically more demanding pushing role on 85% of occasions (FAVILA 1988). However, it is important to note that the male can roll the ball on his own. Whilst having the female may save the male some energy, cooperative transport has probably arisen more as an adjunct to pair formation than for ergonomic benefits and is not a necessity. Similarly, burying beetles (*Nicrophorus* spp.) transport carcasses from patches of hard ground to patches of soft ground for burying. This can be performed individually, with the beetle crawling underneath the carcass and, whilst lying with its back to the ground, levering the carcass forward with its legs. If a mate arrives during transport the pair can cooperate in the transport of the carcass, but again cooperative transport has probably arisen as an adjunct to pair formation than due to the necessity for increase ergonomic benefit (MILNE & MILNE 1976).

MOFFETT (1987) provides second-hand reports of rodent litter mates cooperatively conveying food and of various canid and felid species jointly moving food to shady spots. However, none of these behaviours seem to be common, transport is reported as inefficient and uncoordinated, and we have found no reports published in peer-reviewed literature.

Whilst cooperative transport by individual animals is rare in nature, cooperative transport is in fact extremely common in eukaryotes, but on a microscopic scale. Intracellular transport of vesicles is often performed by multiple molecular motors pulling a single vesicle along microtubules (GROSS & al. 2002). Much as in ants and humans, multiple motors can achieve greater power than individuals, allowing the transport of heavier loads and more rapid load transport (KLUMPP & LIPOWSKY 2005, LIPOWSKY & al. 2010). Cooperative transport by multiple molecular motors also allows longer range transport: Molecular motors will unbind from microtubules sporadically due to thermal noise, so larger groups of transporting motors greatly reduce the probability that all motors become disengaged at once (i.e., cause increased reliability), causing transport to stop (LIPOWSKY & al. 2010).

Why is cooperative transport so rare outside ants and humans? Clearly, many animals are excluded from this behaviour as they are not social. Even amongst cooperating groups there is often much conflict amongst group members (SMITH & SZATHMÁRY 1995), arising from a conflict between maximising individual fitness and collective benefits. In eusocial insects, whilst there may be conflict over re-

production (VISSCHER 1996, RATNIEKS & al. 2006, VAN ZWEDEEN & al. 2007), there is seldom conflict over where resources should be brought to, as all eusocial insects are central place foragers and almost all food items must be brought back to the nest. Selection for cooperation has led to many social insects developing complex and sophisticated communication mechanisms in order to increase colony foraging efficiency (FRISCH 1967, WILSON 1972, SEELEY 1995). Why then do we not see cooperative transport in the other eusocial insects? Bees collect mainly liquids and powders (pollen and nectar) for which there is no need for cooperative transport. Likewise termites either live inside their food source, or cut organic matter into pieces of suitable size for individual transport. Wasps do forage on individual prey items, for which competition may be high. However, wasps fly and the coordination of cooperative transport by two flying carriers might be particularly difficult, especially as an error could result in the item being dropped during flight and likely lost. Indeed, whilst humans use multiple boats or engines to transport items over land or water, the first successful trial of flying cooperative transport was only achieved very recently (MELLINGER & al. 2010), and we are not aware of any large-scale or commercial applications. The constraint against cooperative transport in flight also seems to apply to us. Ants appear to be predominant in the animals in their use of cooperative transport as they have a suite of attributes which make cooperative transport both possible and useful, namely central place foraging among cooperating individuals from the same nest, foraging on foot, and utilizing large food items in habitats with competitors including other ants. The species which do evolve coordinated cooperative transport are those that need to secure items before more dominant species find the item, or species, usually army ants, which benefit from greater transport efficiency when moving items along long trails.

Cooperative transport in robots and simulations

Roboticians have been attempting to achieve cooperative transport by robots for over 25 years (EUSTACE & al. 1993, BAY 1995). Cooperative transport in ants is attractive to roboticians not only because they are the only non-human that effectively transport large loads, but also due to the nature of social insect organisation. The rules used by individual workers can be simple, and so robots based on ants need not be over-complicated. Ants also work in flexible groups, and group performance is generally robust and not greatly affected by changes in the number of individuals or whether all are functioning. In addition, and of great importance, ant groups are self organized and do not require remote control or overseeing (KUBE & BONABEAU 2000, BERMAN & al. 2011). Cooperative transport in ants is also scalable in the number of transporters, is effective at transporting a large range of items, and does not require previous knowledge about the payload to be transported. However, apart from these very general properties, implementations of ant-inspired designs do not generally take inspiration from the specific behaviours of ants (RATNIEKS 2008). In an exceptional case, BERMAN & al. (2011) studied the behaviour of *Aphaenogaster cockerelli* in the lab, and modelled transport in a simulation using qualitative data from their biological studies. They observed, as in previous studies on ants (SUDD 1960, SUDD 1965), that ants respond to

difficulties during carriage by changing their orientation or grasping location. By implementing such behaviour in simulated robots they found that carriage speed increased over time, much as in ants, as individual carriers align themselves in better configurations. However, inspiration is often a two way process, and engineers working on the problem of cooperative transport can provide inspiration for biologists. By formalising the task of collective box-pushing by multiple robots, KUBE & BONABEAU (2000) pose useful questions about cooperative transport. Some of the answers to their questions are known, but others merit future study. Among the questions they raise are: Is worker behaviour in group transport different than in solitary transport? How do several ants cooperate and coordinate their actions to actually transport the item? How does a group of transporting ants handle deadlocks, caused either by the environment or by agonistic behaviours of other transporters? Although partial answers to some of these questions are addressed above, all would benefit from further, formalised study.

Studies of simulated robots tasked with transporting large items can also inform biologists on the evolution of cooperative transport. GROSS & DORIGO (2008) created simulated robots that can move and grasp, but cannot communicate with, or even sense, other simulated robots. By using evolutionary algorithms that select for increased distance that an item is moved, the behaviour of robots was allowed to evolve over multiple rounds of selection. Groß and colleagues investigated whether individuals engaged in cooperative transport can benefit from behaving differently from those engaged in solitary transport. Robot behaviour evolved both in the situation where they had to individually move an object as far as possible, with the object being light enough for one robot to move, and in the situation where the box was too heavy for an individual robot to move, so that multiple robots were needed. They found that robots evolved for cooperative transport did indeed perform better than those which were evolved for individual transport. However, robots evolved for individual transport could nonetheless perform cooperative transport, demonstrating that simple rules designed for individual retrieval can result in cooperative transport, as has been suggested in ants (CHAUVIN 1950, SUDD 1960, CZACZKES & RATNIEKS 2011) (see above). GROSS & DORIGO (2008) also demonstrated that communication amongst individuals during cooperative transport need not be direct, but can arise via individuals changing the state of the environment other individuals interact with, a process known as stigmergy (GRASSÉ 1934). Such evolutionary experiments demonstrate clearly that whilst cooperative transport can arise from behaviours selected for by individual transport, selection specifically for cooperative transport abilities can result in more effective cooperative transport. This echoes the case in real ants, where uncoordinated transport can arise from multiple individuals acting as if they were performing individual transport, but coordinated transport, with its' associated adaptations, is more effective.

Directions for future study

Cooperative transport is, in our opinion, an understudied topic which is worthy of further study. Not only does it provide inspiration for engineers and roboticians, but it also provides an easily manipulated platform for studying the

self-organisation of groups. Many questions about cooperative transport remain unanswered, and puzzling facts remain unexplained. Some closely related species demonstrate very different cooperative transport abilities: *Lasius niger*, for example, does not seem to perform cooperative transport, whilst *L. neoniger* performs efficient cooperative transport of large loads, and indeed collects 85% of its food this way (TRANIELLO 1983). What behavioural traits, adaptations or features are needed to allow cooperative transport to occur? Under which circumstances does coordinated cooperative transport evolve? How do ants sense when they should attempt to assist in cooperative transport or attempt to retrieve an item as an individual? *Pheidologeton diversus* may prove to be an ideal study organism to answer this question, as workers switch between dragging or lifting items using their jaws during individual retrieval to lifting with their head and forelegs during cooperative transport (see Fig. 2). Their body posture effectively signals the state they perceive they are in.

It may also be that the recruitment system of an ant species allows or precludes cooperative transport: Lack of recruitment will prevent ants from achieving cooperative transport, but mass recruitment (with long lasting pheromones), could result in maladaptive recruitment to items long gone. This could perhaps be offset by the use of a "stop" or "no entry" signal (ROBINSON & al. 2005).

Whether or not group members communicate during cooperative transport is still an open question. Stigmergy is likely to play a large role in organisation, as are rules regarding avoiding crowding by both fellow carriers and parts of the item being carried (CZACZKES & al. 2010). However, it is possible that some method of quorum-sensing (PRATT & al. 2002) is employed, either to regulate the number of carriers around an item and prevent further recruitment (HÖLDOBLER & al. 1978), or to signal a change from individual to cooperative transport.

Cooperative transport is a behaviour which is very amenable to study: It is conspicuous, easily manipulated and provides a system in which cooperation and organisation of groups of two to over a hundred can be studied. As cooperative transport does not require direct communication between group members, it is a useful tool for researchers interested in decentralised systems, providing emergent properties which arise within minutes and are performed reliably. Roboticists are beginning to take more direct inspiration from the cooperative transport behaviours of ants, and biologists can in turn take inspiration from work of roboticists on this topic. We hope that this review will provide a useful introduction for others. We look forward to new studies from both biological and engineering perspectives, and studies that combine the two.

Acknowledgements

We thank Mark Moffett, Katja Rex, the Ludwig Maximilians University of Munich Behavioural Ecology group and two anonymous reviewers for comments on previous versions of the manuscript. TC was funded by a BBSRC studentship.

References

ADAMS, E.S. & TRANIELLO, J.F.A. 1981: Chemical interference competition by *Monomorium minimum* (Hymenoptera: Formicidae). – *Oecologia* 51: 265-270.

- ANDERSON, C. & FRANKS, N.R. 2001: Teams in animal societies. – *Behavioral Ecology* 12: 534-540.
- BANSCHBACH, V.S., BRUNELLE, A., BARTLETT, K.M., GRIVETTI, J.Y. & YEAMANS, R.L. 2006: Tool use by the forest ant *Aphaenogaster rudis*: Ecology and task allocation. – *Insectes Sociaux* 53: 463-471.
- BAY, J.S. 1995: Design of the "Army-Ant" cooperative lifting robot. – *Robotics & Automation Magazine, IEEE* 2: 36-43.
- BERMAN, S., LINDSEY, Q., SAKAR, M.S., KUMAR, V. & PRATT, S.C. 2011: Experimental study and modeling of group retrieval in ants as an approach to collective transport in swarm robotic systems. – *Proceedings of the IEEE* 99: 1470-1481.
- BOURKE, A.F.G. & FRANKS, N.R. 1995: *Social evolution in ants*. – Princeton University Press, Princeton, NJ, 529 pp.
- BROCKMANN, H.J. 1985: Tool use in digger wasps (Hymenoptera: Sphecinae). – *Psyche: A Journal of Entomology* 92: 309-329.
- BROSNAN, S.F. & DE WAAL, F.B.M. 2003: Monkeys reject unequal pay. – *Nature* 425: 297-299.
- CARROLL, C. & JANZEN, D.H. 1973: Ecology of foraging by ants. – *Annual Review of Ecology and Systematics* 4: 231-257.
- CERDÁ, X., ANGULO, E., BOULAY, R. & LENOIR, A. 2009: Individual and collective foraging decisions: a field study of worker recruitment in the gypsy ant *Aphaenogaster senilis*. – *Behavioral Ecology and Sociobiology* 63: 551-562.
- CERDÁ, X., RETANA, J. & CROS, S. 1998: Prey size reverses the outcome of interference interactions of scavenger ants. – *Oikos* 82: 99-110.
- CHAUVIN, R. 1950: Le transport des proies chez les fourmis. Y-a-t-il Entr'Aide? – *Behaviour* 2: 249-256.
- CZACZKES, T.J., NOUVELLET, P. & RATNIEKS, F.L.W. 2010: Cooperative food transport in the Neotropical ant, *Pheidole oxyops*. – *Insectes Sociaux* 58: 153-161.
- CZACZKES, T.J. & RATNIEKS, F.L.W. 2011: Simple rules result in the adaptive turning of food items to reduce drag during cooperative food transport in the ant *Pheidole oxyops*. – *Insectes Sociaux* 58: 91-96.
- CZACZKES, T.J. & RATNIEKS, F.L.W. 2012: Pheromone trails in the Brazilian ant *Pheidole oxyops*: extreme properties and dual recruitment action. – *Behavioral Ecology and Sociobiology* 66: 1149-1156.
- DALY-SCHWEITZER, S., BEUGNON, G. & LACHAUD, J. 2007: Prey weight and overwhelming difficulty impact the choice of retrieval strategy in the Neotropical ant *Gnamptogenys sulcata* (F. SMITH). – *Insectes Sociaux* 54: 319-328.
- DETRAIN, C. & DENEUBOURG, J.-L. 1997: Scavenging by *Pheidole pallidula*: a key for understanding decision-making. – *Animal Behaviour* 53: 537-547.
- DJIÉTO-LORDON, C., RICHARD, F., OWONA, C., GIBERNAU, M., ORIVEL, J. & DEJEAN, A. 2001: The predatory behavior of the dominant arboreal ant species *Tetramorium aculeatum* (Hymenoptera: Formicidae). – *Sociobiology* 38: 765-776.
- EUSTACE, D., BARNES, D.P. & GRAY, J.O. 1993: Co-operant mobile robots for industrial applications. – *Industrial Electronics, Control, and Instrumentation* 1: 39-44.
- EVISON, S.E.F., PETCHEY, O.L., BECKERMAN, A.P. & RATNIEKS, F.L.W. 2008: Combined use of pheromone trails and visual landmarks by the common garden ant *Lasius niger*. – *Behavioral Ecology and Sociobiology* 63: 261-267.
- FABRE, J.H. 1911: *The life and love of the insect*. – A&C Black, London, 304 pp.
- FAVILA, M. 1988: Comportamiento durante el periodo de maduración gonádica en un escarabajo rodador (Coleoptera: Scarabaeidae; Scarabaeinae). – *Folia Entomologica Mexicana* 76: 55-64.

- FINN, J.K., TREGENZA, T. & NORMAN, M.D. 2009: Defensive tool use in a coconut-carrying octopus. – *Current Biology* 19: R1069-R1070.
- FRANKS, N.R. 1986: Teams in social insects: group retrieval of prey by army ants (*Eciton burchelli*, Hymenoptera: Formicidae). – *Behavioural Ecology and Sociobiology* 18: 425-429.
- FRANKS, N.R., SENDOVA-FRANKS, A.B. & ANDERSON, C. 2001: Division of labour within teams of New World and Old World army ants. – *Animal Behaviour* 62: 635-642.
- FRANKS, N.R., SENDOVA-FRANKS, A.B., SIMMONS, J. & MOGIE, M. 1999: Convergent evolution, superefficient teams and tempo in Old and New World army ants. – *Proceedings of the Royal Society B-Biological Sciences* 266: 1697-1701.
- FRISCH, K. VON 1967: The dance language and orientation of bees. – Harvard University Press, Cambridge, MA, 566 pp.
- GOODALL, J. 1964: Tool-using and aimed throwing in a community of free-living chimpanzees. – *Nature* 201: 1264-1266.
- GRASSÉ, P. 1934: Comment la fourmi fileuse *Oecophylla smaragdina* FAB. trouve-t-elle sa nourriture. – *Bulletin de la Société entomologique de France* 10: 151-153.
- GROSS, S.P., WELTE, M.A., BLOCK, S.M. & WIESCHAUS, E.F. 2002: Coordination of opposite-polarity microtubule motors. – *The Journal of Cell Biology* 156: 715.
- GROSS, R. & DORIGO, M. 2008: Evolution of solitary and group transport behaviors for autonomous robots capable of self-assembling. – *Adaptive Behavior* 16: 285-305.
- GRÜTER, C., CZACZKES, T.J. & RATNIEKS, F.L.W. 2011: Decision making in ant foragers (*Lasius niger*) facing conflicting private and social information. – *Behavioral Ecology and Sociobiology* 64: 141-148.
- HALFFTER, G. 1997: Subsocial behavior in Scarabaeinae beetles. In: *The evolution of social behavior in insects and arachnids*. – Cambridge University Press, Cambridge, UK, pp. 223-259.
- HARRISON, J.F., FEWELL, J.H., STILLER, T.M. & BREED, M.D. 1989: Effects of experience on use of orientation cues in the giant tropical ant. – *Animal Behaviour* 37: 869-871.
- HÖLDOBLER, B. 1981: Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* WHEELER (Hymenoptera: Formicidae). – *Behavioral Ecology and Sociobiology* 9: 301-314.
- HÖLDOBLER, B., STANTON, R.C. & MARKL, H. 1978: Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera): I. chemical signals. – *Behavioral Ecology and Sociobiology* 4: 163-181.
- HÖLDOBLER, B. & WILSON, E.O. 1990: The ants. – Harvard University Press, Cambridge, MA, 732 pp.
- HÖLDOBLER, B. & WILSON, E.O. 2009: The super-organism: the beauty, elegance, and strangeness of insect societies. 1st edition. – W.W. Norton & Co., New York, NY, 544 pp.
- HUNT, G.R. 1996: Manufacture and use of hook-tools by New Caledonian crows. – *Nature* 379: 249-251.
- JACKSON, D.E., MARTIN, S.J., HOLCOMBE, M. & RATNIEKS, F.L.W. 2006: Longevity and detection of persistent foraging trails in Pharaoh's ants, *Monomorium pharaonis* (L.). – *Animal Behaviour* 71: 351-359.
- KLUMPP, S. & LIPOWSKY, R. 2005: Cooperative cargo transport by several molecular motors. – *Proceedings of the National Academy of Sciences of the United States of America* 102: 17284-17289.
- KUBE, C.R. & BONABEAU, E. 2000: Cooperative transport by ants and robots. – *Robotics and Autonomous Systems* 30: 85-101.
- LIPOWSKY, R., BEEG, J., DIMOVA, R., KLUMPP, S. & MÜLLER, M.J.I. 2010: Cooperative behavior of molecular motors: cargo transport and traffic phenomena. – *Physica E: Low-dimensional Systems and Nanostructures* 42: 649-661.
- MASCHWITZ, U. & STEGHAUS-KOVAC, S. 1991: Individualismus versus Kooperation. – *Naturwissenschaften* 78: 103-113.
- MASUKO, K. 1990: Behavior and ecology of the enigmatic ant *Leptanilla japonica* BARONI URBANI (Hymenoptera: Formicidae: Leptanillinae). – *Insectes Sociaux* 37: 31-57.
- MELLINGER, D., SHOMIN, M., MICHAEL, N. & KUMAR, V. 2010: Cooperative grasping and transport using multiple quadrupots. In: *Proceedings of the International Symposium on Distributed Autonomous Robotic Systems*. – <<http://www.seas.upenn.edu/~dmel/mellingerDARS10.pdf>> retrieved on 28 March 2012.
- MILNE, L.J. & MILNE, M. 1976: The social behavior of burying beetles. – *Scientific American* 235: 84-89.
- MOFFETT, M.W. 1986: Notes on the behavior of the dimorphic ant *Oligomyrmex overbecki* (Hymenoptera: Formicidae). – *Psyche: A Journal of Entomology* 93: 107-116.
- MOFFETT, M.W. 1987: Sociobiology of the ants of the genus *Pheidologeton*. – PhD thesis, Harvard University, Cambridge, MA, 284 pp.
- MOFFETT, M.W. 1988: Cooperative food transport by an Asiatic ant. – *National Geographic Research and Exploration* 4: 386-394.
- MOFFETT, M.W. 1992: Ant foraging. – *National Geographic Research and Exploration* 8: 220-231.
- MOFFETT, M.W. 2010: Chapter 5: In: *Adventures among ants: a global safari with a cast of trillions*. – University of California Press, Berkeley, CA, 288 pp.
- OSTER, G.F. & WILSON, E.O. 1978: Caste and ecology in the social insects. – Princeton University Press, Princeton, NJ, 352 pp.
- PAŠKO, Ľ. 2010: Tool-like behavior in the sixbar wrasse, *Thalassoma hardwicke* (BENNETT, 1830). – *Zoo Biology* 29: 767-773.
- POWELL, S. & FRANKS, N.R. 2005: Caste evolution and ecology: a special worker for novel prey. – *Proceedings of the Royal Society B-Biological Sciences* 272: 2173-2180.
- POWELL, S. & FRANKS, N.R. 2006: Ecology and the evolution of worker morphological diversity: a comparative analysis with *Eciton* army ants. – *Functional Ecology* 20: 1105-1114.
- PRATT, S.C. 1989: Recruitment and other communication behavior in the ponerine ant *Ectatomma ruidum*. – *Ethology* 81: 313-331.
- PRATT, S.C., MALLON, E., SUMPTER, D. & FRANKS, N.R. 2002: Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. – *Behavioral Ecology and Sociobiology* 52: 117-127.
- RABAUD, E. 1937: Phénomène social et sociétés animales. – Felix Alcan, Paris, XI + 322 pp.
- RANGE, F., HORN, L., VIRANYI, Z. & HUBER, L. 2009: The absence of reward induces inequity aversion in dogs. – *Proceedings of the National Academy of Sciences of the United States of America* 106: 340-345.
- RATNIEKS, F.L.W. 2008: Biomimicry: further insights from ant colonies? In: LIÒ, P., YONEKI, E., CROWCROFT, J. & VERMA, D.C. (Eds.): *Bio-inspired computing and communication*. – Springer, Berlin, Heidelberg, pp. 58-66.
- RATNIEKS, F.L.W., FOSTER, K.R. & WENSELEERS, T. 2006: Conflict resolution in insect societies. – *Annual Review of Entomology* 51: 581-608.
- RICHARD, F.J., FABRE, A. & DEJEAN, A. 2001: Predatory behavior in dominant arboreal ant species: the case of *Crematogaster* sp. (Hymenoptera: Formicidae). – *Journal of Insect Behavior* 14: 271-282.
- ROBINSON, E.J.H., JACKSON, D.E., HOLCOMBE, M. & RATNIEKS, F.L.W. 2005: Insect communication: "No entry" signal in ant foraging. – *Nature* 438: 442.
- ROBSON, S.K. & TRANIELLO, J.F.A. 1998: Resource assessment, recruitment behavior, and organization of cooperative prey re-

- retrieval in the ant *Formica schaufussi* (Hymenoptera: Formicidae). – *Journal of Insect Behavior* 11: 1-22.
- ROBSON, S.K. & TRANIELLO, J.F.A. 2002: Transient division of labour and behavioural specialization in the ant *Formica schaufussi*. – *Naturwissenschaften* 89: 128-131.
- SCHNEIRLA, T.C. 1933: Studies on army ants in Panama. – *Journal of Comparative Psychology* 15: 267-299.
- SEELEY, T.D. 1995: The wisdom of the hive: the social physiology of honey bee colonies. – Harvard University Press, Cambridge, MA, 323 pp.
- SMITH, J.M. & SZATHMÁRY, E. 1995: The major transitions in evolution. – Oxford University Press, Oxford, 346 pp.
- SUDD, J.H. 1960: The transport of prey by an ant, *Pheidole crassinoda* Em. – *Behaviour* 16: 295-308.
- SUDD, J.H. 1965: Transport of prey by ants. – *Behaviour* 15: 234-271.
- TOFFIN, S. 2003: Étude expérimentale du transport collectif chez la fourmi *Pheidole pallidula*. – PhD thesis, Université Libre de Bruxelles, Brussels, 52 pp.
- TRANIELLO, J.F.A. 1983: Social organization and foraging success in *Lasius neoniger* (Hymenoptera: Formicidae): behavioral and ecological aspects of recruitment communication. – *Oecologia* 59: 94-100.
- TRANIELLO, J.F.A. 1987: Comparative foraging ecology of north temperate ants: the role of worker size and cooperative foraging in prey selection. – *Insectes Sociaux* 34: 118-130.
- TRANIELLO, J.F.A. 1989: Foraging strategies of ants. – *Annual Review of Entomology* 34: 191-210.
- TRANIELLO, J.F.A. & BESHERS, S.N. 1991: Maximization of foraging efficiency and resource defense by group retrieval in the ant *Formica schaufussi*. – *Behavioral Ecology and Sociobiology* 29: 283-289.
- VAKANAS, G. & KRAFFT, B. 2004: Regulation of the number of spiders participating in collective prey transport in the social spider *Anelosimus eximius* (Araneae, Theridiidae). – *Comptes Rendus Biologies* 327: 763-772.
- VISSCHER, P.K. 1996: Reproductive conflict in honey bees: a stalemate of worker egg-laying and policing. – *Behavioral Ecology and Sociobiology* 39: 237-244.
- WILSON, E.O. 1972: The insect societies. – Harvard University Press, Cambridge, MA, 562 pp.
- WITTE, V., SCHLISSMANN, D. & HASHIM, R. 2010: Attack or call for help? Rapid individual decisions in a group-hunting ant. – *Behavioral Ecology* 21: 1040-1047.
- YAMAMOTO, A., ISHIHARA, S. & ITO, F. 2009: Fragmentation or transportation: mode of large-prey retrieval in arboreal and ground nesting ants. – *Journal of Insect Behavior* 22: 1-11.
- VAN ZWEDEN, J.S., FÜRST, M.A., HEINZE, J. & D'ETTORRE, P. 2007: Specialization in policing behaviour among workers in the ant *Pachycondyla inversa*. – *Proceedings of the Royal Society B-Biological Sciences* 274: 1421-1428.