

# Cooperative food transport in the Neotropical ant, *Pheidole oxyops*

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**Abstract** Cooperation in foraging through information sharing is widespread in social insects and has been much studied. In contrast, cooperative transport of food items by groups of workers is less common and has received comparatively little attention. We investigated collective food retrieval in the Neotropical ant *Pheidole oxyops*, a ground-nesting species in which minor workers (mean body weight 0.6 mg) collectively transport larger dead insects back to the nest entrance. In total, 29% of items and 78% of total mass is transported collectively. We examined the configurations of ants carrying single experimental food items (weight 119 mg, size 10 × 10 × 1 mm) and found it to be non-random, with twice as many carrying ants at the corners as expected. This arrangement is achieved by preferential joining of corners and leaving of sides by carriers. Corner carrying increased carrying speed by up to 29%. Ants also preferentially carried food items from the front and back, versus the middle.

**Keywords** Cooperative transport · Foraging behaviour · Ants · Organisation · Group transport

## Introduction

Social insects stand out in the extent and complexity of their cooperative behaviour. Cooperation among workers is

involved in many areas of colony life, such as nest building (Franks et al., 1992; Deneubourg and Franks, 1995), defence (Frehland et al., 1985; Hölldobler and Wilson, 1990), hygienic behaviour (Hart and Ratnieks, 2002), and especially foraging (Hölldobler and Wilson, 1990; Robson and Traniello, 2002). Foraging in ants differs to that of bees and wasps in that ants must forage and retrieve food on foot. This allows ants many unique foraging behaviours, such as cooperative retrieval of food items.

Cooperative retrieval of single food items by groups of ants is common though not universal, is documented in 40 genera of ants and has arisen independently many times (Hölldobler and Wilson, 1990; Moffett, 2010). It may result in “superefficient” groups, in which multiple ants can collectively carry a larger weight than would be manageable if divided amongst the individual workers (Sudd, 1965; Franks, 1986; Moffett, 1988; Deneubourg and Beshers, 1991; Franks et al., 1999, 2001; Robson and Traniello, 1998). Cooperative transport can also help reduce inter-specific interference (Cerdá et al., 1998; Deneubourg and Beshers, 1991).

Several aspects of cooperative transport have been well studied to date, including the mechanism of carrier number recruitment optimisation (Franks, 1986; Traniello, 1983), the composition of retrieval groups (Franks, 1986; Franks et al., 1999), and the ecological significance of group retrieval (Deneubourg and Beshers, 1991; Yamamoto et al., 2009; Schatz et al., 1997; Detrain, 1990). Much less work has investigated the coordination and arrangement of carriers. Chauvin (1971) notes that *Formica polyctena* are excited by, and more likely to grasp, moving objects and objects surrounded by con-specifics, which leads to cooperative transport. Sudd (1965) showed that small groups (mean ca. 3 ants) of *F. lugubris* did not position themselves at random around a cooperatively transported prey item, and

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eventually began pulling in the same direction, although achieving coordination could take a pair of ants as long as 10 min.

The most detailed studies of cooperative transport in ants have been carried out on army ants (Franks, 1986; Franks et al., 1999, 2001; Powell and Franks, 2005). Franks (1986) describes the formation of coordinated teams of new world army ants, *Eciton burchelli*. These typically involve one submajor and one or more smaller workers. The larger submajor carries the food item from the front slung underneath her body, with the smaller worker(s) lifting the rear to reduce drag (Powell and Franks, 2005). Franks et al. (2001) describe similar teams in the old world army ant *Dorylus wilverthi*. These army ant examples represent highly sophisticated examples of carrying in species with polymorphic workers. Powell and Franks (2005) suggest that the emergence of the specialist carrier caste in *E. burchelli* arose as a direct consequence of the shift to taking large arthropod prey. Franks and colleagues provide a detailed description of the organisation of prey carriers in these highly specialised, polymorphic species. This study aims to be a counterpoint to these studies, presenting data on cooperative transport in a species with monomorphic carriers that regularly work in groups of four or more, which will be relevant to many other cooperative carriers. Several studies on cooperative transport in less polymorphic ant species investigate recruitment behaviour (Detrain and Deneubourg, 1997; Cerdá et al., 2009) or group size adjustment (Robson and Traniello, 1998), but few examine the arrangement of carriers during transport. A handful of studies do describe the arrangement of carriers (Sudd, 1960, 1965; Moffett, 1988), but the general conclusion seems to be that, excluding army ants, ants collectively transporting a large food item tend to work more as solitary foragers, taking no account of the efforts of their sisters. This results in uncoordinated actions such as pulling in opposite directions until, by chance, the ants are pulling in the same direction and transport can resume (Sudd, 1965). One study by Moffett (1988) on the swarm raiding ant *Pheidologeton diversus* reports coordinated cooperative transport, but does not provide data on the organisation of the carriers.

In this study, we investigate cooperative food retrieval behaviour by minor workers in the Neotropical ant *Pheidole oxyops*. Cooperative transport is important in this species, with 78% of prey retrieved this way (see below). Our results show that minor workers are not distributed at random around an experimental food item, but rather are over-represented at the corners and that this increases retrieval speed. In addition, we investigate the mechanisms governing ant distribution around an experimental food item during retrieval and show that more ants carry by the leading side than the trailing side, and more ants carry by the trailing edge than by any one of the sides.

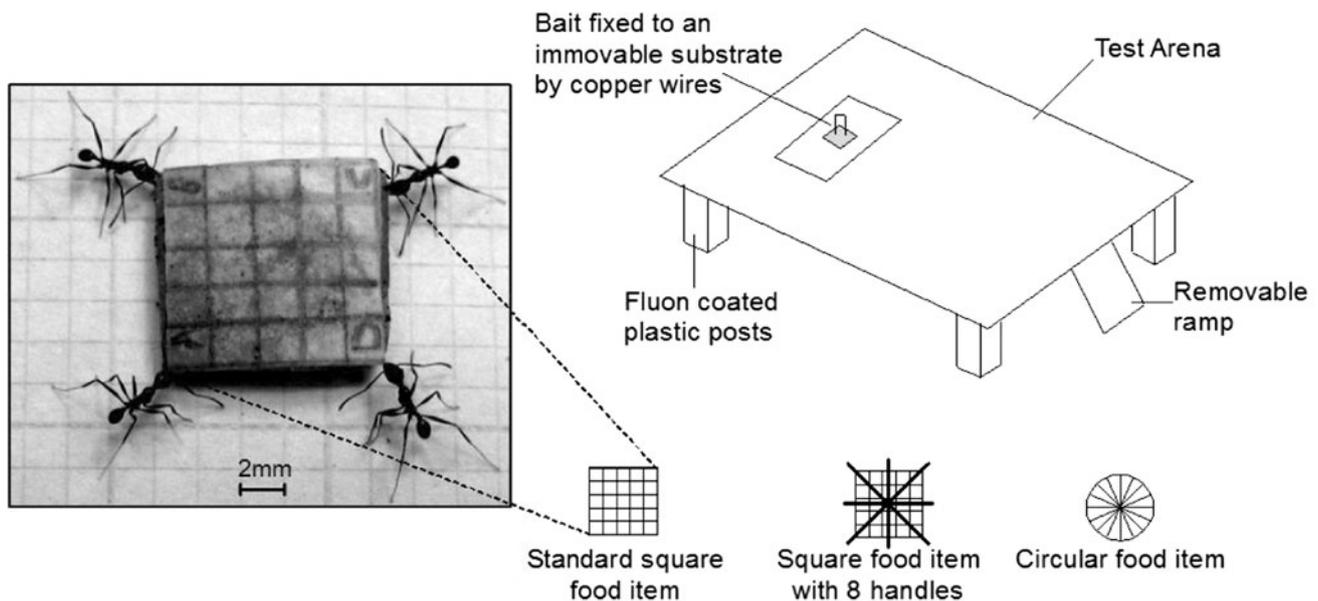
## Methods and results

### Site and study organism

Data were collected between January 29, 2009 and February 28, 2010 at Fazenda Aretuzina, near São Simão, São Paulo State, Brazil. Air temperatures ranged from 23 to 31°C. The study species, *P. oxyops*, is dimorphic, with large headed major workers [mean body mass 61.6 mg, SD 11.2 mg,  $n = 20$  (5 from each of 4 colonies)] and small-headed minor workers (body mass 6.0 mg, SD 1.7 mg,  $n$  as above). Majors were never observed to be involved in natural foraging. *P. oxyops* nest in the ground and hunt and scavenge for prey, which are often carried back by multiple workers.

We chose to study *P. oxyops* as they display group recruitment from the nest and coordinated cooperative transport, which is a major aspect of their foraging behaviour. During 5 h of observation on 9 colonies (33 min per colony), 103 food items were collected, 69% of which were arthropods. 29% of all food items, accounting for 78% of total food mass, were transported cooperatively by minor workers. Average group size was 3.5 individuals, (SE = 0.84), with the largest group observed being 30 ants retrieving a mantid approximately 50 mm long. Average load mass of individually carried items was 0.0023 g (SE = 0.0003) and for cooperatively transported items was 0.0874 (SE = 0.0711). Heavier items were more likely to be cooperatively transported (Spearman's rank correlation,  $\rho = 0.604$ ,  $df = 131$ ,  $P < 0.001$ ). A worker who is unable to move a food item is able to cause the recruitment of many additional nestmate workers to the item from the nest, as occurs in several other ant species (Hölldobler et al., 1978; Schatz et al., 1997; Robson and Traniello, 1998; Daly-Schweitzer et al., 2007; Amor et al., 2010; Cerdá et al., 2009). Foraging occurred during daytime and all data were collected from 0900 to 1800. Data were not collected during and for at least an hour after rain as this disrupted foraging.

To maintain consistency, all data were collected in the shade, either under tree cover or a parasol, and within 0.5 m of the nest entrance using test arenas consisting of an A4 (210 × 297 mm) sheet of 2-mm graph paper backed by a tile (Fig. 1). The arena was raised 40 mm off the ground on polytetrafluoroethylene-coated plastic posts with access provided by a cardboard ramp fixed to the side closest to the nest entrance. The standard food item, used in all experiments except 6, was a 10 × 10 × 1 mm piece of cheese overlaid with 2-mm graph paper, weighing in total 119 mg. The perimeter, where the ants would grasp the item, was divided into 20 2-mm edge sectors, 2 at each corner and 3 along each side (Fig. 1). Our operational definition of a corner was the two sectors meeting at a corner point. This was large enough for two ants to simultaneously grasp a



**Fig. 1** Basic set up of apparatus, and representations of the three food item types used. Photograph shows four ants cooperatively carrying a standard food item by the corners. The food item is a  $10 \times 10 \times 1$  mm piece of mozzarella cheese weighing ca. 119 mg overlaid by a 2-mm grid

corner, which occasionally occurred. Group recruitment for cooperative transport is initiated when a worker is unable to retrieve a food item due to too-high tractive resistance (see above). Thus, a wave of ants could be directed onto the test arena by offering an immovable food item at the far end of the arena to trigger recruitment.

#### Experiment 1: effect of carrier number on carriage speed

##### Method

The aim of this experiment was to determine the relationship between the number of carrier ants and the carriage speed of a food item. A colony was presented with a standard food item on the test arena. Recruitment was triggered using a fixed  $5 \times 5$  mm food bait. Forager ants were then presented with a standard food item and allowed to carry it towards the nest. All ants not holding the food item were brushed off the test arena. On reaching the nestward side of the test arena, the item was replaced in its original position at the far end of the test arena using a pair of soft forceps. Any ants that fell off the item were removed from the arena, and the item was allowed to be carried towards the nest again. This was repeated until no ants remained, which never took longer than 15 min. Whilst resulting in non-independence of data, this allowed large sample sizes, and no group was used more than three times. A minimum of five repeats with different ants were carried out for each group size. Temperature was measured every trial using a

bulb thermometer placed by the test arena. Data were collected from colony A.

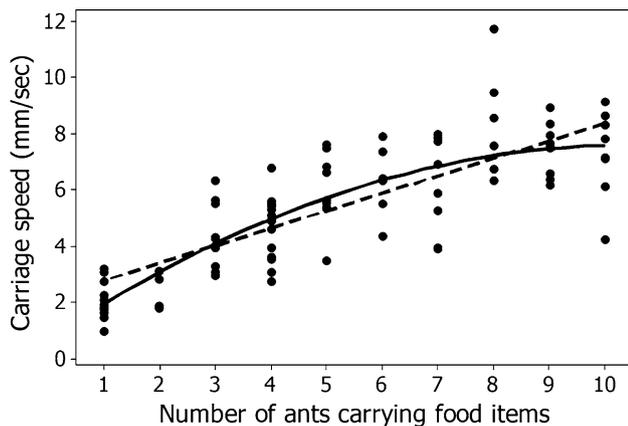
##### Results

A single ant could just drag our standard food item. Carriage speed increased with more ants but levelled off at approximately 5–7 ants (Fig. 2). A quadratic regression explains significantly more of the variation than a linear regression (sequential ANOVA,  $df = 1$ ,  $F = 12.01$ ,  $P < 0.05$ ) showing that the relationship is non-linear. The best fit quadratic equation was carriage speed (mm per s) =  $0.6764 + 1.325n - 0.06328n^2$  (quadratic regression,  $F = 12.18$ ,  $df = 88$ , adjusted  $R^2 = 67.9\%$ ,  $P < 0.001$ ), which fits the data better than the linear regression ( $F = 156.25$ ,  $df = 88$ , adjusted  $R^2 = 63.8\%$ ,  $P < 0.001$ ). Temperature had a significant effect on carriage speed but explained  $<5\%$  of the variation in speed (linear regression,  $T = 2.28$ ,  $df = 88$ , adjusted  $R^2 = 4.6\%$ ,  $P = 0.025$ ).

#### Experiment 2: distribution of carriers

##### Method

This experiment investigated whether ants distribute themselves randomly around a standard food item on a raised arena. Following the results of Experiment 1, we studied groups of four ants in this and other experiments as four carrier ants could move the food item and yet was



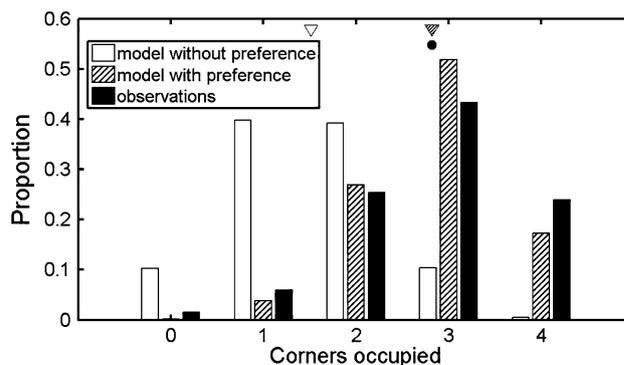
**Fig. 2** Effect of the number of ants carrying an experimental food item, a  $10 \times 10 \times 1$  mm piece of mozzarella cheese weighing ca. 119 mg, on carriage speed. Quadratic regression line: speed (mm/s) =  $0.6764 + 1.325n - 0.06328n^2$  ( $S = 0.127$ , adjusted  $R^2 = 67.9\%$ ,  $P = 0.001$ ). Linear regression line (dashed): speed =  $2.073 + 0.6301n$  ( $S = 1.71$ , adjusted  $R^2 = 63.8$ ,  $P < 0.001$ )

below the number of carriers at which the number to speed relationship levelled off (see Experiment 1). As such, we expected that carriage speed with four ants would be sensitive to the positions of the carrier ants around the food item. Ants were allowed to carry the item for 2 min. Whenever the ants came close to the edge of the test arena they were allowed to walk onto a piece of card and replaced in the centre of the arena. After 2 min in which ants could adjust their distribution around the food item, a photograph was taken to determine the number of corners occupied. Colonies A ( $N = 22$ ), B ( $N = 19$ ) and C ( $N = 26$ ), were studied.

We compared the observed distribution of ants at corners versus middle sectors against the expected distributions based on random choice of middle versus corner sectors (see supplementary material Appendix A). Given that the food item was a 10 mm square, its perimeter is 40 mm, and the expected random probability of joining a corner is  $0.4$  ( $(4 \times 4)/40$ ).

## Results

Figure 3 shows that the distribution of ants was non-random. An average of 2.8 corners were occupied, compared to 1.5 for the model that best fit the observational data but did not include a preference for corners (see supplementary material Appendix A). Only by adjusting the model so that ants were allowed to have a preference for corners was it possible to obtain an expected distribution that did not differ significantly from observed (G test:  $G = 6$ ,  $df = 3$ ,  $P = 0.108$ ). In this model, ants cannot share a sector nor a corner (formed of two sectors) and had a preference for joining corner sectors over side sectors ( $P_c$  = probability of



**Fig. 3** Proportion of corners occupied by a carrying ant. Black bars are observed data, white bars represent the model where ants have no preference for corners and cannot share corner or side sectors. The hatched bars represent the model where ants cannot share corner or side sectors and corner sectors are 5.4 times more likely to be occupied than side sectors (see Appendix A). The triangles and circle represent the means of the models and observation, respectively

joining one of the corner, estimated by maximum likelihood  $P_c = 0.196$ , 95% CI 0.184, 0.207; see supplementary material Appendix A). As ants have been observed to occasionally share a sector, the likely situation is that the chance of joining a sector drops dramatically to a low but non-zero value when it is already occupied by one ant. However, for the purposes of this study, the simpler models suffice to demonstrate corner preference.

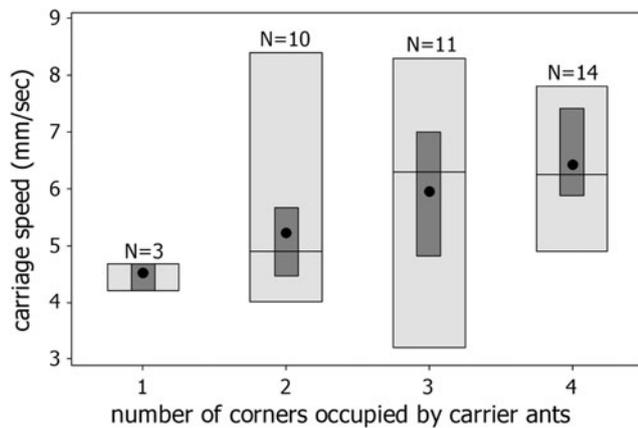
## Experiment 3: effect of ant distribution on carriage speed

### Method

Basic methods followed Experiment 2. The four ants were allowed to walk for up to 2 min, or until they had carried the food item for a minimum of 30 mm without stopping or turning. Trials were video recorded and a single measurement of carriage speed and the number of corners occupied at that time was taken from each video. Colonies A ( $N = 18$ ), and C ( $N = 20$ ), were studied.

### Results

As significant differences were found between the two colonies, colonies were analysed separately. Carriage speed increases significantly with the proportion of corners occupied in colony C (Spearman's Rank Correlation,  $df = 18$ ,  $\rho = 0.716$ ,  $P < 0.001$ ), whilst the trend was similar but not significant in colony A (Spearman's rank correlation,  $df = 16$ ,  $\rho = 0.270$ ,  $P = 0.185$ ). Figure 4 shows pooled results for both colonies, and shows walking speed of 4.5, 5.2, 6.0 and 6.4 mm/s for 1, 2, 3 and 4 occupied corners, respectively. When less than four corners are



**Fig. 4** Carriage speeds (mm/s) of  $10 \times 10 \times 1$  mm 119-mg food items being carried by four ants depending on how many of the corners of the food item have one or more ants grasping them. *Bisecting lines* indicate medians, *circles* indicate means, *light boxes* indicate interquartile range, and *dark boxes* indicate 95% confidence interval for the median

occupied the remaining ants are either carrying at a side sector or co-occupying a corner.

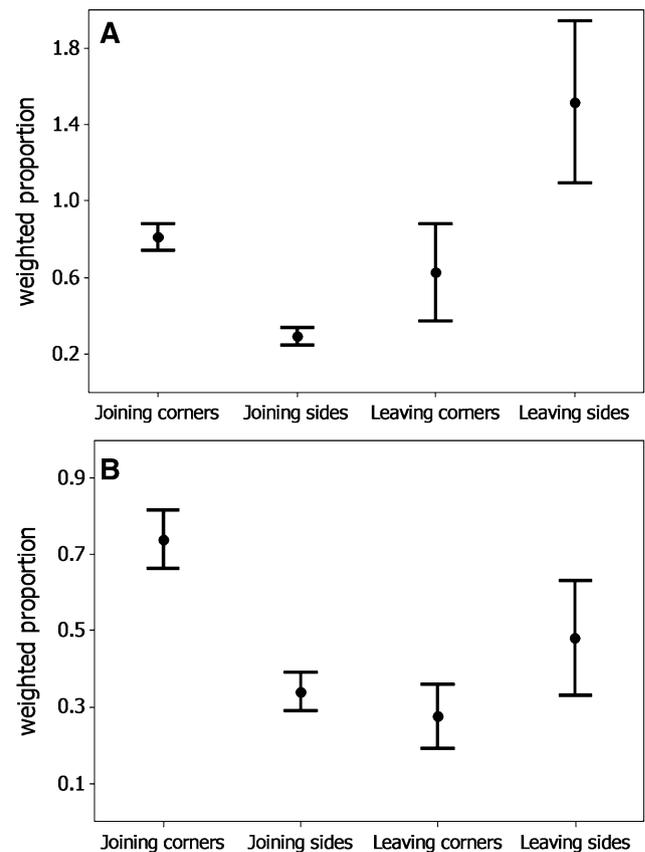
#### Experiment 4: mechanism of ant distribution adjustment

##### Method

Basic methods followed Experiments 2 and 3. A group of four carrier ants was video recorded for 1 min after the food item first started moving. Instances of joining and leaving at corners and sides were recorded, and rates of joining and leaving calculated. Colonies A ( $N = 12$ ), B ( $N = 11$ ) and C ( $N = 13$ ), were studied. An event was defined as a single act of joining or leaving. For example, if an ant joins onto a side, lets go, and then joins a corner there are three events. Ants were considered to have joined when they clearly grasped the food item with their mandibles and remained at a fixed position on the food item for at least 1 s. So as to get a measure of the how long ants grasp the corners and sides, the duration for which each of the four ants grasped the item for the first time was measured. Only the first grasping event was measured to insure that no ant was measured twice. Ants that had not released the item by the end of the video were assigned a grasping duration of 60 s.

##### Results

The proportion of joining events on corners and sides was calculated and weighted to reflect the larger proportion of side sectors. The proportion of leaving events on corner and side sectors was weighted by the proportion of joining events for corners and sides. Figure 5a shows that ants join the corners at a significantly higher rate than the



**Fig. 5** Weighted proportions of ants joining and leaving corners and sides of a  $10 \times 10 \times 1$  mm food item, without (a) ( $N = 36$ ) and with (b) ( $N = 46$ ) handles. *Circles* indicate mean, *lines* indicate 95% confidence intervals for the medians

sides (mean  $\pm$  SD-weighted proportion of joining events  $0.81 \pm 0.20$  vs.  $0.29 \pm 0.14$ ; two sample  $t$  test  $t = 9.15$ ,  $P < 0.001$ ,  $N = 36$ ) and leave the sides at a significantly higher rate than the corners (mean weighted proportion of leaving events  $0.63 \pm 0.74$  vs.  $1.52 \pm 1.25$ ; two sample  $t$  test  $t = -4.12$ ,  $P < 0.001$ ,  $N = 36$ ). Ants grasped the corners of the item significantly longer than the sides (Kruskal–Wallis,  $N$  corners = 65,  $N$  sides = 43,  $Z = 4.05$ ,  $P < 0.001$ ).

#### Experiment 5: ant distribution on food items with additional “handles”

##### Method

By making the sides of a food item as easy to grasp as the corners, this experiment investigated the possibility that corners might be preferred simply because they are easier to grasp than sides. The general method is identical to Experiment 4. Four copper wires, diameter ca. 0.3 mm, were attached to a standard food item to give 8 2-mm handles around the perimeter of the food item. Two wires

were diagonals, protruding 2 mm from the corners, and two were placed perpendicular, protruding from the centres of the sides (Fig. 1). Ants readily grasped these handles when carrying a food item. Colonies A ( $N = 17$ ), B ( $N = 12$ ) and C ( $N = 17$ ), were studied. Grasping duration was also measured as above.

## Results

Again the proportion of joining and leaving events were weighted and compared as above. When the food items were given handles on both corners and sides, ants still joined corners more than sides (mean  $\pm$  SD-weighted proportion of joining events  $0.74 \pm 0.26$  vs.  $0.34 \pm 0.17$ ; two sample  $t$  test  $t = 3.85$ ,  $P < 0.001$ ,  $N = 35$ ) (Fig. 5b) and left the sides at a higher rate than the corners (mean  $\pm$  SD-weighted proportion of leaving events  $0.28 \pm 0.28$  vs.  $0.48 \pm 0.51$ ; two sample  $t$  test  $t = -2.1$ ,  $P < 0.043$ ,  $N = 35$ ). There was a non-significant trend for ants to grasp the corners longer than the sides (Kruskal–Wallis,  $N$  corners = 60,  $N$  sides = 62,  $Z = 1.72$ ,  $P = 0.069$  adjusted for ties). When comparing ant behaviour around food items with and without handles, there was no significant difference in joining rates of corners or sides (two sample  $t$  test, sides:  $df = 79$ ,  $t = 0.139$ ,  $P = 0.169$ ; corners:  $df = 79$ ,  $t = 0.139$ ,  $P = 0.169$ ) but leaving rates were reduced when handles were provided (two sample  $t$  test, sides:  $df = 44$ ,  $t = 4.7$ ,  $P < 0.001$ ; corners:  $df = 42$ ,  $t = 2.7$ ,  $P = 0.01$ ).

## Experiment 6: joining rules for a moving food item

### Method

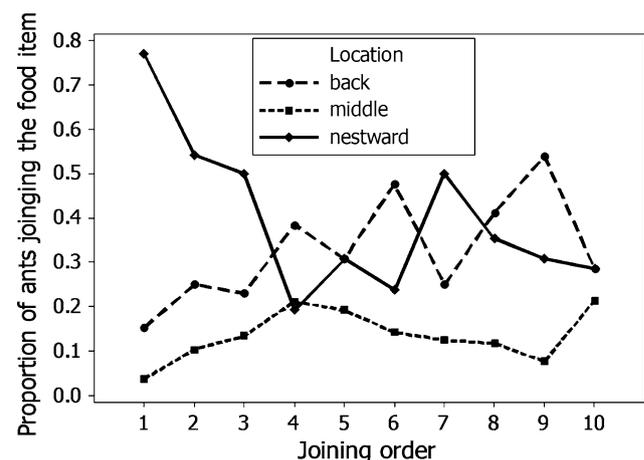
This experiment investigated the order in which ants joined different locations of an already moving food item in relation to the direction of the nest entrance and the movement of the item (i.e., facing the entrance, facing away). To eliminate any preference for corners over sides, a circular food item 10 mm in diameter was used. The perimeter was marked into 16 equal sectors. The test arena was lowered to allow access from all sides of the arena. The carriage of the food item was video recorded until it was carried off the arena, a distance of 280 mm. Ants were classified as joining the nestward side if they joined one of the four sectors facing towards the nest, the back if they joined one of the opposite four sectors, and the middle if they joined one of the eight intermediate sectors. Ants were ranked according to joining order independent of the number of ants already grasping the food item. Colonies A ( $N = 10$ ) and C ( $N = 16$ ) were studied. At the end of each video the number of ants carrying by the nestward, middle and back sectors was counted.

## Results

The first three ants to join joined the nestward side of a food item at a significantly higher rate than the back or sides (ANOVA,  $df = 233$ ,  $F = 22.09$ ,  $P < 0.001$ : 77% (variance = 18.5) of the first ants to join a food item joined the nestward side, versus 15% (variance = 13.5) for the far side and 8% (variance = 13.5) for the two middle sides combined. As the nestward side became occupied, more ants started joining the middle and back (Fig. 6). Proportionally more ants joined the nestward side or back than the sides, and over the entire carriage period ants joined the nestward side and back equally (two sample  $t$  test, nestward vs. middle,  $t = 4.21$ ,  $P = 0.002$ , back vs. middle,  $t = 4.51$ ,  $P = 0.001$ , nestward vs. back,  $t = 1.08$ ,  $P = 0.299$ ). All ants seemed to carry the item nestwards, with the ants at the back walking forwards, those at the front walking backwards, and those at the middle walking sideways. By the end of the observation period more ants carried from the nestward side than from the back, and more ants carried from the back than the middle (front mean = 2.8, SD = 0.80, back mean 2.09, SD = 0.98, middle mean/2 = 1.6, SD = 0.56. One way ANOVA for difference  $df = 104$ ,  $F = 19.14$ ,  $P < 0.001$ , adjusted  $R^2 = 25.86\%$ ).

### Statistical analysis

All statistical analyses were carried out using Minitab 14 unless stated otherwise. Specific tests are given in the results sections. All tests were two tailed unless stated otherwise. Data from different colonies were pooled where no significant difference among colonies was found using an ANOVA. Significant colony effects were only found in experiment 3, where colonies were analysed



**Fig. 6** Proportion of ants joining the nestward, middle and back sectors of a mobile circular food item, 10 mm diameter, by the order in which the ants join and begin to help transport the item

separately. Maximum likelihood estimations were performed on Matlab.

## Discussion

Our results show that the organisation of cooperative food transport of large items in *P. oxyops* has features that appear to increase food transport effectiveness. There is a strong preference for carrying by the corners, and this leads to higher carriage speeds. In addition, the position that carrying ants join the food item is also non-random with regard to food item position relative to the nest. A mechanism for adjustment of carrying positions is provided by varying rates of joining and leaving the carried item. These findings demonstrate some sophistication in the organisation of cooperative carrying.

When only one corner is occupied the mean carriage speed is only 70% of the speed when all four corners are occupied. This gives a possible adaptive explanation for the behaviours observed in Experiments 2 and 5, which show that ants preferentially carry food items by the corners. Faster prey retrieval could have several benefits, such as reducing the time the ants are at risk from predation, desiccation and interference from competitors, and the freeing up of workers for other tasks (Feener and Moss, 1990; Tanner, 2008; Cerdá et al., 2009).

The non-random distribution of ants found in Experiment 2 arises in part due to different joining and leaving rates for sides versus corners and in part due to ants remaining at corners longer than sides (Experiment 4): ants joined corners at a rate 1.75 times that of sides and left sides at a rate 1.2 times that of corners, and remained at corners 50% longer. Experiment 5 demonstrated that the preference for joining corners cannot simply be explained by corners being easier to grasp: Even when the food items had additional handles at both sides and corners ants joined the corners at 1.4 times the side rate. After weighting the proportion of leaving events by the proportion of joining events, ants were also found to leave the sides at a higher rate than corners. Therefore, there is probably something intrinsic about a corner that is attractive to the ants. The fact that the addition of handles decreased leaving rates of corners and sides whilst not changing joining rates suggests that the reason ants join an area may not be the same reasons it chooses to stay or leave.

This study also raises the mechanistic question of how ants sense a corner.  $10 \times 10$  mm pieces of cheese are notably absent from most ecosystems, and clear  $90^\circ$  corners along with them. What is it about corners that causes a preference? We demonstrated that a corner is not sensed only by the ease by which it is grasped, by showing that corners are preferred even when the sides are equally easy to

grasp (Experiment 5). There are several possible explanations for the preference of ants to carry by the corners. Corners may simply be contacted more easily, or carrying by the corner may be more efficient as the food item, and possibly other ants, do not get in the way of the ants' legs so much (Fig. 1). Lifting part of a pliable food item by a corner may be easier than lifting by a side, and would result in reduced surface exposure to the substrate and thus reduced friction. Lastly, Czaczkes and Ratnieks (2010) showed that during the turning of food items to reduce drag, most ants causing the turning grasped the item by the corner. Grasping items by a corner provides greater leverage for turning the item. Experiment 3 clearly shows that faster carriage speed is one advantage of carrying by the corners. This may also explain Sudd's (1965) finding that *F. lugubris* workers tend to arrange themselves around a food item in an over-dispersed manner. Therefore, we suggest that ants simply have a preference for grasping a food item where they will be least crowded, both by their sisters and by parts of the food item itself.

Experiment 6 explored the joining behaviour of ants around a circular food item currently being transported. At first, ants preferentially joined the nestward side. As this became more occupied the back was preferentially joined over the middle (Fig. 6). This is not what one would expect if ants, when finding the front sectors fully occupied, simply moved to the next free space, as this would be the middle. Thus, this tendency to join the back of an item versus the middle probably arises from a direct preference. *P. oxyops* workers appear to walk in a coordinated manner towards the nest, with ants at the front pulling and ants at the back pushing and lifting, similar to behaviour reported by Moffett (1988) but in contrast to the uncoordinated behaviour of *Myrmica rubra* and *F. lugubris* reported by Sudd (1965). Carrying and walking sideways may be more difficult and thus might be less preferred. Carrying from the sides may also be disfavoured as, if unbalanced by ants on both sides, it could cause imbalance in the carrying force. These results have parallels with teams of army ants retrieving prey (Franks, 1986). The larger ant carrying from the front in army ants can be compared to a group of workers in *P. oxyops*. In both cases, a large amount of ant-power is directed at carrying from the front, and may be assisted by a smaller amount of ant-power lifting at the back (Experiment 5).

Ants must carry a variety of objects, and the method by which they carry is determined by the shape and mass of the object to be carried. Leaf cutter ants, for example, cut pieces of leaves and fruit to be carried resulting in items that can be carried by a single media ant holding the item above its body, although the item size is usually below peak efficiency (Rudolph and Loudon, 1986; Burd, 1996). Army ants dissect larger prey items and often carry the resulting items back in cooperative teams of two to four ants, the larger

workers holding the food item slung underneath its body and the smaller workers lifting the item from behind (Franks et al., 2001). For ants species that are more susceptible to disruption from other ants dissection is maladaptive, and bulky items are more likely to be retrieved without dissection (Yamamoto et al., 2009), as occurs in our study species, *P. oxyops*.

Cooperative transport by similar individuals of bulky items that cannot be dissected is a common problem for both ants and humans, so the study of such systems may be of importance for both ant behaviour and technological application. Indeed, the study of how similar individuals cooperatively solve complex tasks is finding applications in current and future technology (Woern et al., 2006; Christodoulou, 2009). Cooperatively carrying a load by robots may be improved and informed by insights from ant behaviour. Cooperative pushing, pulling and towing have been achieved several times using “swarms” of independent robots (Kube and Bonabeau, 2000; Pettinaro et al., 2005; Wang and de Silva, 2006; Udomkun and Tangamchit, 2008). Real world applications may also require lifting, especially of delicate items or work on irregular terrain, and lessons learned from this and future studies may provide inspiration for solving such lifting problems. The benefits of ant-inspired systems may be of prime importance in robotic applications where direct intervention is impossible or impractical, such as deep sea or extraterrestrial engineering (Huntsberger et al., 2000; Parker and Zhang, 2006; Woern et al., 2006). Cooperatively lifting objects is something that humans and their machines need to do regularly. Although at an early stage, insights from cooperative transport by ants, and ant behaviour in general, may have far reaching applications.

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**Conflict of interest** The authors declare that they have no conflict of interest.

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