# RESEARCH ARTICLE

## Do ants need to be old and experienced to teach?

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### SUMMARY

**Learning is widespread in invertebrates. However, whether social insects improve their recruitment skills with experience is only beginning to be investigated. Tandem running is a one-to-one form of recruitment used by certain species of ant. It is a remarkable communication system that meets widely accepted criteria for teaching in non-human animals. Here, we determined experimentally to what extent participation in, and efficient execution of, tandem running depends on either the age or the experience of worker ants. To investigate these issues, we constructed colonies of the ant *Temnothorax albipennis* with different compositions of inexperienced and experienced workers from different age cohorts and then examined which ants participated in tandem runs when they emigrated. Our results show that the ability to participate actively in recruitment by tandem running is present in all worker age groups but the propensity to participate varies with experience rather than age *per se*. Experienced individuals were more likely to engage in tandem runs, either as leaders or as followers, than young inexperienced individuals, and older experienced ants were more likely to lead tandems than older inexperienced ants. Young inexperienced ants led faster, more rapidly dispersing and less accurately orientated tandem runs than the older experienced ants. Our study suggests that experience (rather than age *per se*) coupled to stimulus threshold responses might interact to promote a division of labour so that a suitable number of workers actively participate in tandem runs.**

## INTRODUCTION

Learning is widespread in insects (Dukas, 2008). For example, many insects learn landmarks to help them navigate in both directions between their nests and foraging sites (Collett et al., 2003; Fukushi and Wehner, 2004). It is therefore not implausible that certain insects might improve their ability to perform certain tasks, i.e. to acquire or improve particular skills. Here, we began to investigate this issue for a particular form of recruitment communication in ants. Skill refinement, if it occurs in ants, might also have consequences for their division of labour as rapid accomplishment of certain tasks might prevent others from having the opportunity to practise them.

The ecological success of social insects can be attributed, in part, to efficiencies that accrue from the division of labour in their colonies (Hölldobler and Wilson, 1990; Robinson, 1992). How different workers allocate themselves to tasks is a major focus in ant ergonomics (Oster and Wilson, 1978). There are several hypotheses concerned with how division of labour is maintained in social insect colonies and although they differ in emphasis they are not necessarily mutually exclusive. One important hypothesis is age polyethism, according to which workers begin their employment within the nest before moving, as a consequence of their age, to more dangerous tasks outside the nest (Hölldobler and Wilson, 1990; Robinson, 1992). Task choices are also known to be influenced by physiological differences among individuals (Robinson, 2009),

such as corpulence (Blanchard et al., 2000; Toth and Robinson, 2005; Robinson et al., 2009a) and an individual's life expectancy, and hence its corresponding value to the colony (Porter and Jorgensen, 1981; Moroń et al., 2007; Tofilski, 2009). Differences in the response thresholds of individuals, such that some will begin tasks at certain stimulus levels that others will ignore, could also promote the division of labour (Bonabeau et al., 1996; Beshers and Fewell, 2001). A worker's threshold for taking up a task could be influenced by many factors such as experience, development or repeated exposure to stimuli (Riveros and Gronenberg, 2010; Tofts and Franks, 1992; Franks and Tofts, 1994; Gronenberg et al., 1996; Seid and Traniello, 2006; Ravary et al., 2007). To investigate the contributions of these influences, we tested the effects of worker age and experience on tandem running in the rock ant *Temnothorax albipennis*.

Tandem running is a behaviour in which one worker leads a single follower to a goal such as food or a new nest site, pausing if the follower loses contact (Wilson, 1959; Franks and Richardson, 2006). Tandem running is often deployed to build a small but massively influential group of informed ants that can quickly carry the rest of the colony (queen, brood and passive workers) to a new nest. Tandem running might be expected to be the social domain of the oldest and/or most experienced workers for three reasons. First, in *T. albipennis* tandem running has a pivotal role in new nest choice

(Pratt et al., 2002); such decisions are likely to influence the inclusive fitness of all colony members, so it would benefit the colony to have the most able individuals performing this task. Second, tandem running is such a sophisticated form of communication that it actually qualifies as a form of teaching (Franks and Richardson, 2006; Richardson et al., 2007). Indeed, it trains other recruiters because followers of tandem runs often become leaders of subsequent tandem runs (Möglich et al., 1974; Franks and Richardson, 2006; Richardson et al., 2007). Moreover, a colony might benefit if the leaders of tandem runs are more effective at transferring information by achieving the best compromise between accuracy and speed. Third, tandem running recruits ants to new food sources or new nest sites and it is such a remarkably slow, ponderous and predictable behaviour that it is likely to expose its participants to predators more than any other extra-nidal behaviour (Franks and Richardson, 2006). Therefore, to maximize inclusive fitness one might expect participation in tandem runs to be the exclusive preserve of older ants. This is because such ants are likely to have more experience of foraging and navigation. Moreover, as tandem running is perilous, the loss of older ants might be less costly to the colony, in the long term, because they would have a lower life expectancy and they are typically leaner than younger ants (Porter and Jorgensen, 1981; Moroń et al., 2007; Robinson et al., 2009b; Tofilski, 2009).

For these three reasons, tandem running might be performed primarily by older or more experienced workers. Indeed, young workers might have a lower propensity to participate in tandem runs or a lower frequency of participation because: (1) their physiological development is insufficient (Seid et al., 2005; Seid and Traniello, 2006); (2) they have higher response thresholds (Bonabeau et al., 1996); or (3) they are inhibited or excluded by older workers (Wilson, 1985).

Separating the effects of age and experience on task performance is challenging because they often go hand in hand – gaining experience takes time and is therefore coupled with age. So, in an ideal world one might wish to compare all permutations of young, old, experienced and inexperienced workers. However, whereas it may be possible to uncouple age and experience by denying older individuals the opportunity to practise certain skills, it might well be virtually impossible for individuals to be both young and experienced as gaining experience takes time. Moreover, both age and experience are concerned with how the past shapes the present and therefore one needs long-term information on the histories of individuals. Notwithstanding such challenges, these are important issues, especially in social insects, in which the division of labour may be associated with age and/or experience.

To begin to resolve some of these issues with regard to the influence of age and experience on the division of labour in ants, we constructed artificial colonies with workers in different age cohorts and with different degrees of experience and considered a task – tandem running – which is, in our study species, both important and rare, only occurring in particular circumstances. By contrast, if we had chosen an everyday task we could not have controlled the exposure of workers to it. Thus by considering a rare task, we could control when members of colonies had the opportunity to perform the task in question and in turn influence how much experience workers had at performing such a task.

To discriminate between the influences of age and experience, we examined the different combinations of participants in tandem runs and their comparative efficiencies (speed, dispersal and accuracy) in emigrating colonies with controlled ratios of younger inexperienced and older experienced workers.

## MATERIALS AND METHODS
### Collection and culturing of colonies

Complete, queen-right *T. albipennis* (Curtis 1854) donor colonies ($N$=50) were collected from a coastal site in Dorset, UK, in 2007 and 2008. The colonies were housed in nests consisting of a 2 mm thick cardboard perimeter between $75 \times 50$ mm microscope slides. The nesting cavity in the cardboard was $35 \times 50$ mm with a 2 mm wide and 6 mm long entrance. We cultured all of the ant colonies in small Petri dishes and provided them with *ad libitum* access to a 1:10 honey–water solution, dead *Drosophila* and water. These resources were placed close to the nest so that tandem runs were not induced during foraging, preventing uncontrolled experience of tandem running.

### Participation

To determine whether worker age or experience or both influence participation in tandem runs we needed to construct artificial colonies in which we could control the demographic structure of their populations of workers and the experience or inexperience of such workers in tandem runs. To examine the role of workers of different age and experience in tandem runs, we then conducted emigration experiments involving: (1) only young and inexperienced (YI) workers ($N$=50), (2) only old and inexperienced (OI) workers ($N$=50), (3) a mixture of YI ($N$=50) and old and experienced (OE) workers ($N$=10).

To produce YI workers, colonies collected in the field in 2007 and 2008 ($N$=50) were incubated at 28°C during the day (09:00 h–17:00 h) and at 21°C overnight, to induce the production of callows (newly eclosed worker ants). The young workers were harvested from the donor colonies when they were 7–30 days old. The YI workers we used in the participation experiments were produced in 2009. All were individually marked and individual ant identity could be assured.

We derived the OI workers from YI workers produced in the laboratory in 2008. The OI workers were 10±1 months old in 2009 and for at least 9±1 months had not participated in any emigrations (although they had experience of emigrations when they were much younger, Fig. 1A). Typically emigrating colonies only produce about 10 tandem runs per emigration in relatively small
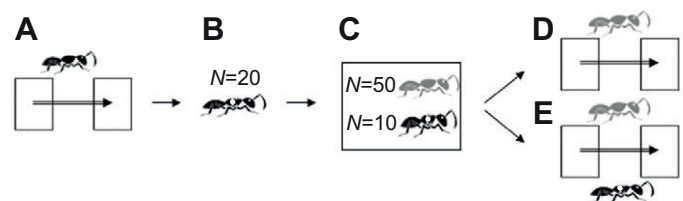


Fig. 1. A diagram to illustrate how the artificial colonies were constructed and used in emigrations. (A) Seven artificial colonies of 50 individually marked old inexperienced (OI) ants emigrate (Table 1, row i). These ants were produced from former young inexperienced (YI) ants that had not emigrated for at least 9 months. (B) Six sets of 20 OI ants that participated in tandem running, either as a leader or as a follower, were randomly selected from all tandem participants. These six sets are old experienced (OE) ants. (C) The six sets of 20 OE ants were randomly assigned to groups of 10–12 artificial colonies containing 50 YI workers. YI ants were selected from several unemigrated colonies. All ants were individually marked. (D) The YI ants in four of the 12 colonies emigrate in the absence of OE ants (Table 1, row ii). (E) The YI and OE ants in the remaining eight colonies emigrate together (Table 1, rows iii and iv). Black ants, OI; black ants with white dot, OE; grey ants, YI. Arrows with a double shaft indicate colony emigration.

arenas (E.L.F., unpublished observations), so it is unlikely that anything more than a small minority of these OI workers had played an active role in any tandem runs and it is especially unlikely that after more than 9 months they would have remembered the characteristics of the experimental arena, even though it was the same arena in the same location. As Langridge and colleagues have shown, *T. albipennis* colonies no longer emigrate quickly if 1 week elapses between successive emigrations, even though in these experiments too the arena was kept constant and in the same location (Langridge et al., 2004). In addition, 10 month old workers are unlikely to have begun to senesce because individual workers can live for 6 years in the laboratory (A.B.S.-F., unpublished observations).

We selected OE workers in 2009 from the YI workers produced in 2008, after using their emigrations as OI workers as 'training', i.e. as a source of recent and extensive experience (Fig. 1B). For this training, the ants were individually marked, so that we could record the participation of each individual in tandem runs (either as a leader or as a follower; for ratios of participation in tandem runs, see Table 1, row i). This allowed us later to use ants that had actively participated in tandem running as our OE individuals. We subsequently chose a subset of the OE ants to be assigned at random as the 10 OE ants in colonies with 50 YI ants.

There were seven sets of 50 OI workers and each was emigrated four times. Potentially, each worker could act as a leader or a follower. This gives a total of 7×4×50×2=2800 possible participations (Table 1, row i). All of the OI workers were given 7 days rest before being integrated into a constructed experimental colony as OE workers.

The YI workers produced in 2009 and the OE workers were combined in 12 queen-less experimental colonies each consisting of 50 individually marked YI individuals and 10 individually marked OE individuals (Fig. 1C). The YI workers in four of these colonies were emigrated four times in the absence of the OE workers (Fig. 1D). This gives a total of 4×4×50×2=1600 possible participations for YI workers (Table 1, row ii). The YI workers were emigrated together with the OE workers three times in the remaining eight colonies and a fourth time in four of the remaining eight colonies (Fig. 1E). This gives a total of (8×3×50×2) + (4×1×50×2)=2800 possible participations for YI workers (Table 1, row iii) and a total of (8×3×10×2) + (4×1×10×2)=560 possible participations for OE workers (Table 1, row iv).

All the colonies we constructed also had small numbers of brood items (median 20.5, range 11–32).

When a series of four emigrations was used, they all occurred within a 6 day period to facilitate the ants learning to emigrate extremely efficiently (Langridge et al., 2004). All experienced or mature individuals who were removed before an emigration were reunited with their colony when the emigration had been completed.

### Efficiency

To investigate efficiency, as measured by analyses of mean speed, dispersal and mean orientation, we used only data from first emigrations. The first emigration data were used to ensure ants could only use knowledge of the arena gained in that emigration. To evaluate the basic ability of ants to lead tandem runs, we compared YI ants leading YI ants *versus* OE ants leading YI ants. For this analysis, we used data for four sets of 50 YI workers produced in 2008 that emigrated in the absence of experienced nestmates in 2008, and the 2009 data for 12 sets of 50 YI workers, of which four sets emigrated in the absence and eight emigrated in the presence of 10 OE workers.

Emigrations were recorded on mini DV tapes with a Sony HDV Handycam (HDR-FX1E). Tandem run videos were digitized using Adobe Premier Pro 2.0 and played back on Windows Media Player Classic. The paths of tandem leading ants were tracked by manually plotting their positions on a grid in second by second increments. We used the Cell Counter plugin in Image J (Rasband, 1997–2005) to obtain the co-ordinates of every increment to digitize each tandem path. From these data we were able to calculate mean instantaneous speed (the mean of all time increments for each tandem) and the mean square dispersal rates of tandems (Nouvellet et al., 2009). We used the mean square displacement statistic, which has been shown to be a fundamental quantity in measuring the dispersal of correlated random walks (Nouvellet et al., 2009). We tested for normality of displacements, required by the statistic of Nouvellet and colleagues (Nouvellet et al., 2009), using the method they describe (see their eqn 5); this analysis of our data indicated that displacements were indeed normally distributed. As our data showed mean square displacement increasing in proportion to $t^2$ (where $t$ is time), we divided the statistic by $t$ to enable a linear regression on time, as suggested previously (Nouvellet et al., 2009). Given this $t^2$ relationship, the root mean square displacement statistic used previously (Franks et al., 2010) gives qualitatively identical results,

Table 1. Results from the participation experiments

| Rows (with worker age and experience) | Leaders | Followers | Non-participants | Total |
|---|---|---|---|---|
| (i) 50 OI workers | **41** | **64** | **2695** | **2800** |
| Expected frequency | 40.05 | 50.52 | 2709.43 | |
| Chi-squared contribution | 0.022 | 3.600 | 0.077 | |
| (ii) 50 YI workers | **18** | **24** | **1558** | **1600** |
| Expected frequency | 22.89 | 28.87 | 1548.25 | |
| Chi-squared contribution | 1.043 | 0.820 | 0.061 | |
| (iii) 50 YI workers in the presence of 10 OE workers | **27** | **44** | **2729** | **2800** |
| Expected frequency | 40.05 | 50.52 | 2709.43 | |
| Chi-squared contribution | 4.253 | 0.840 | 0.141 | |
| (iv) 10 OE workers in the presence of 50 YI workers | **25** | **8** | **527** | **560** |
| Expected frequency | 8.01 | 10.10 | 541.89 | |
| Chi-squared contribution | 36.035 | 0.438 | 0.409 | |
| Total | **111** | **140** | **7509** | **7760** |

All ants had individual paint marks. Individuals were only counted once as a leader and once as a follower in an emigration even if they participated in many tandem runs. The total number of ants is doubled as each ant has the opportunity to be both a leader and a follower in each emigration.
Bold indicates observed values, and row and column totals.
OI, old inexperienced; OE, old experienced; YI, young inexperienced.

save for differences in the linear regression constants. We also only analysed the dispersal data up until the maximum observed displacement. We compared the dispersal slopes by calculating the 95% confidence intervals (CIs) for the gradient and checking for overlap (gradient±$t_{0.025v}$×s.e.m. for gradient, where v=d.f.=sample size−2). We folded the 360 deg mean angle data of tandem routes into 180 deg to combine the trajectories to the two experimental nests (see below) and to facilitate analysis. In our analysis the new nest was at 90 deg.

### Emigration protocol

We conducted the emigration experiments during July–December 2008 and May–December 2009. Although all our constructed experimental colonies were queen-less, in *T. albipennis* no differences have been detected in the behaviour of queen-less and queen-right colonies during emigrations (Franks et al., 2003a; Dornhaus and Franks, 2006).

A 520×840 mm arena with Fluon®-coated walls (to prevent the ants escaping) was used, in the same location, for all the emigrations. It was cleaned with ethanol before every experiment to remove any previously deployed pheromones. Two new nests, with cavities shaded from the light by a cover so the ants would prefer them to their current nest (Franks et al., 2003a; Franks et al., 2003b; Franks et al., 2006), were placed symmetrically 280 mm from the central initially inhabited nest. Each new nest was covered with a square upturned Petri dish (100×100 mm). Each such Petri dish had one small hole in its far side to allow access and to increase route complexity, thus increasing the number of tandem runs. Observations of tandem runs were made only until ants were in line with the closest edge of a Petri dish. We did this to eliminate the effects of differences in routes caused by the Petri dish. Emigrations were induced by removing the top slide of the old nest and ended when the old nest had been completely vacated.

Minitab (Minitab Ltd, Coventry, UK) was used for the statistical analyses and Oriana version 1.06 (1994, Warren L. Kovach, Kovach Computing Services, Pentraeth, Wales, UK) for the angular statistics.

## RESULTS
### Participation

The frequency of participation in tandem runs either as followers or as leaders differs significantly between the treatments (Table 1, heterogeneity test chi-squared=47.740, d.f.=6, *P*<0.001). Indeed, inspection of all of the cell-by-cell chi-squared contributions shows all rows and all columns (except that for non-participation) contribute to the observed heterogeneity. Given this, we can now assess the relative roles of age and experience by comparing certain combinations of pairs of rows from this overall table.

Comparison of the data for OI ants and YI ants (Table 1, row i *versus* row ii; supplementary material Table S1A) shows, all else being equal, no significant effect (chi-squared=4.15, d.f.=2, *P*=0.126) of age *per se* on participation in tandem runs. By contrast, comparison of results from YI and OE ants within colonies composed of both types of ant (Table 1, row iii *versus* row iv; supplementary material Table S1B) shows that YI ants are capable of leading and following tandem runs but suggests that they lead tandem runs less frequently than the OE ants (chi-squared=37.543, d.f.=2, *P*<0.001). Nevertheless, the YI ants and the OE ants were equally likely to follow tandem runs. Comparing rows iii and iv of Table 1 (see supplementary material Table S1B) with a chi-squared test provides expected values of 43 and 9 for participation as followers in tandem runs by the YI and OE ants, respectively, and these match the respective observed frequencies of 44 and 8 very closely indeed.

To address the question of whether YI ants are inhibited or excluded from leading tandem runs by the presence of OE workers, we can compare single cohorts of YI ants with YI ants that are in the presence of OE ants (i.e. Table 1, rows ii and iii; supplementary material Table S1C). The analysis shows no significant effects of these treatments (chi-squared=0.292, d.f.=2, *P*=0.864). This suggests that YI ants are not inhibited or excluded from leading tandem runs by the presence of OE workers.

Finally, we can compare OE ants in the presence of YI ants with single cohorts of OI ants (i.e. Table 1, row iv *versus* row i; supplementary material Table S1D). This shows a significant effect of these treatments (chi-squared=23.205, d.f.=2, *P*<0.001). Comparing rows i and iv of Table 1 (see supplementary material Table S1D) with a chi-squared test provides expected values of 55 and 11 for participation as leaders by OI and OE, respectively, and these are strikingly different to the respective observed frequencies of 41 and 25. Indeed, OE ants lead tandem runs more than twice as frequently as expected. These results suggest that experience might increase the propensity of ants to lead tandem runs. All the significant results above remain significant after the application of Bonferroni correction, whereby the corrected significance level α′=0.05/3=0.017. A denominator of 3 is used in this correction because each data set is used in, at most, three comparisons.

In summary, our main findings are: (1) that YI ants can both lead and follow tandem runs; (2) there is no significant effect of age *per se* on frequency of participation in tandem runs by inexperienced ants; (3) but experienced (and hence older) ants show a significantly increased propensity to lead tandem runs. Thus, taken together, the results in Table 1 and supplementary material Table S1 suggest that experience may increase the propensity of individuals to lead tandem runs and is more important than age *per se* in terms of participation in tandem runs.

### Efficiency

To evaluate the basic ability of ants to lead tandem runs, we compared YI ants leading YI ants *versus* OE ants leading YI ants. When the YI individuals were leading, tandems had significantly faster mean instantaneous speeds (one-way ANOVA, $F_{1,64}$=15.74, *P*<0.001, Fig. 2). Tandems led by YI workers had a significantly higher rate of dispersal from their point of origin [mean dispersal rate=3.850 mm s$^{-1}$, 95% CI=(3.792, 3.908), *N*=85] than those led by OE workers [mean dispersal rate =0.534 mm s$^{-1}$, 95% CI=(0.517,
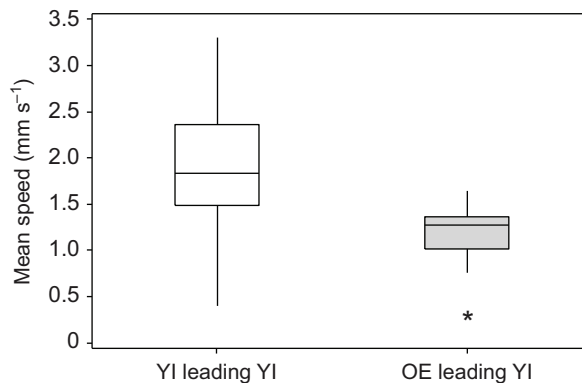


Fig. 2. Box plot showing the mean speed of tandems, comparing YI ants leading YI ants (*N*=51) and OE ants leading YI ants (*N*=15). The central line within the box is the median while the box encloses the inter-quartile range, whiskers show the 1.5 times inter-quartile range and outliers are marked with an asterisk.
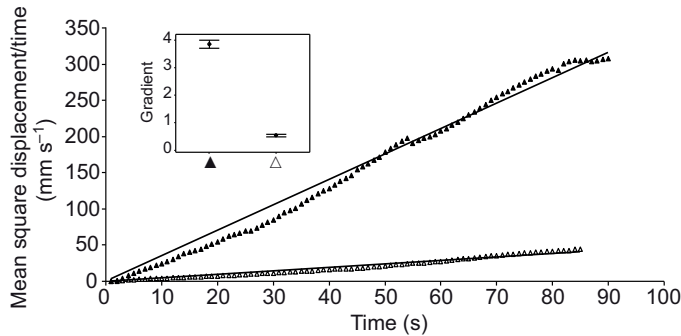
Fig. 3. The rate of mean square displacement from the path origins for tandem runs led by either YI (*N*=51) or OE workers (*N*=15). Filled triangles represent tandems that involved a YI ant led by a YI ant; open triangles represent tandems that involved a YI ant led by an OE ant. Each point represents the mean over all tandems of the respective type for the corresponding second; the solid lines show the line of best fit for each of the two relationships. The inset is an interval plot showing the 95% confidence intervals for the gradient.

0.551), *N*=85, Fig. 3]. In general, tandems led by OE ants were more accurately orientated towards a new nest than tandems led by YI workers. Tandems led by YI workers deviated on average 27 deg from the target of the new nest. This is a significant deviation because here the 95% CI does not contain the target (Fig. 4A). By contrast, tandems led by OE workers deviated on average only 5 deg from the direct bearing of the new nest. This deviation is not significant because the 95% CI contains the target (Fig. 4B). Directly comparing the bearings of tandem runs led by experienced and inexperienced workers shows that they are significantly different (Watson–Williams *F*-test, $F_{1,64}$=5.663, *P*=0.02, Fig. 4).

## DISCUSSION

YI ants participate in tandem runs as leaders or as followers just as readily as do 10 month OI ants. This suggests that age *per se* has little influence on the propensity to participate in tandem runs and that necessity drives participation. However, in colonies constructed to have a cohort of YI ants and a much smaller group of OE workers, tandem runs are mostly led by the experienced (and incidentally older) workers. These results need to be considered with caution, however, because the OE workers were chosen from ants that had already shown a propensity to tandem run (i.e. to have participated at least once as a leader or a follower). Selecting ants that we had observed to participate in tandem running was the only way to ensure that our OE individuals were indeed experienced. However, we chose such ants randomly and because there are more individuals

that act as followers rather than as leaders, our sample would have been expected to contain more followers than leaders. Notwithstanding this, the results show a strong tendency for OE individuals to act as leaders. In addition, the propensity to follow tandem runs seems to be remarkably similar across all of the workforce. Moreover, YI workers do not seem to be inhibited or excluded from leading tandem runs by the presence of OE and disproportionately active workers. It is the experience gained by the OI individuals in becoming OE individuals that seems to have increased their propensity to lead tandem runs. It thus seems likely that YI workers simply have intrinsically higher response thresholds for leading tandem runs than experienced (and incidentally older) workers.

Taken together, these results suggest that experience rather than age *per se* is more important in terms of the propensity of workers to participate in, and especially to lead, tandem runs. Nevertheless, the flexibility of having YI workers that can lead tandem runs is likely to be beneficial if for whatever reason more experienced workers are not available.

We also found that tandem runs led by more experienced workers are generally better at precisely targeting their goal and that they proceed more slowly than those led by inexperienced workers. This would be consistent with experienced workers having learnt that slow steady progress facilitates the maintenance of follower contact. Experienced ants may also be more practised at assimilating navigational information and this might translate into more accurate tandem runs. In other words, there might be two factors at work here; one is navigational expertise, the other is expertise in the mechanics of leading tandem runs. As the same arena was used in the same location in all of our experiments, experienced tandem leaders might have had a greater propensity to engage in such behaviour again because of their improved likelihood of successfully finding the target. In addition, experienced tandem leaders might have improved skills in interacting successfully with tandem followers and this might also increase their propensity to engage in this role.

In principle, the faster tandem speeds of the YI workers could be advantageous, deleterious or neutral. Faster tandems could mean quicker access to the new nest or fewer breaks during runs, but they could also represent wasted energy or possibly a need to run faster to overcome poor path choices. Another distinct possibility is that the speed of the YI tandem leaders could be detrimental to the learning of the follower. The 'lesson' might be being taught too quickly, disrupting the full uptake of information by the follower (Franks and Richardson, 2006). Unfortunately, in all our experiments there were only six cases where a follower went on to become a leader, two from the 2009 emigrations of YI workers only and four
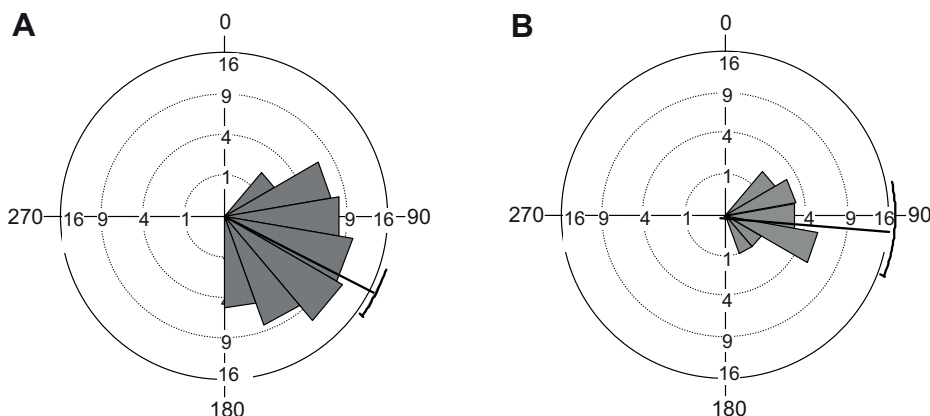


Fig. 4. Histograms of the mean angle of orientation of YI ants leading YI workers (A, *N*=51) or OE ants leading YI workers in tandems (B, *N*=15). The 360 deg data are folded into 180 deg to combine paths to both nests and facilitate analysis. The new nests would be located at 90 deg. The T-bar shows the mean heading with the crossbar displaying the 95% confidence intervals.

from the experimental training of OI to OE workers in 2009. Therefore, we cannot rigorously compare the quality of the 'lessons' taught. This low frequency of social information transfer is probably an artefact of the small colonies we used reaching the quorum threshold number (the number of ants to transport the rest of the colony) quickly because it represents only a small proportion of the total colony size (Pratt et al., 2002; Pratt, 2005). It is also possible that specialization rather than efficiency (Dornhaus, 2008; Muscedere et al., 2009) explains why experienced workers typically lead tandem runs. More experienced (and incidentally generally older) ants could be more active or have a lower life expectancy, which might influence their tendency to participate.

We have shown that, even without experience, young ants are capable of performing successful tandem runs on their first attempt. This may help colonies if, for whatever reason, experienced (and incidentally older) workers are missing. Such flexibility in the division of labour is to be expected especially in small ant colonies in capricious habitats (Bourke and Franks, 1995; Dornhaus et al., 2009).

It is perhaps not so surprising that experience matters in tandem running. This finding is fully consistent with our earlier work showing the extraordinary sophistication of communication in tandem running, with bi-directional feedback between the leader and the follower (Franks and Richardson, 2006), three forms of evaluation (Richardson et al., 2007), the ability of followers to extrapolate successfully from incomplete tandem runs (Franks et al., 2010), and even the ability of physically (Richardson et al., 2007) or visually disabled workers (Franklin et al., 2011) to tune their behaviour to one another during tandem runs. Tandem running may involve many innate elements but the algorithm of this fascinating communication also seems to be fine tuned by experience. So it would appear that in tandem running in ants, teaching is influenced both by nature and by nurture.

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Table S1. Participation in tandem runs

| Rows (with worker age and experience) | Leaders | Followers | Non-participants | Total |
|---|---|---|---|---|
| **A** | | | | |
| (i) 50 OI workers | **41** | **64** | **2695** | **2800** |
| Expected frequency | 37.55 | 56.00 | 2706.45 | |
| Chi-squared contribution | 0.318 | 1.143 | 0.048 | |
| (ii) 50 YI workers | **18** | **24** | **1558** | **1600** |
| Expected frequency | 21.45 | 32.00 | 1546.55 | |
| Chi-squared contribution | 0.556 | 2.000 | 0.085 | |
| Total | **59** | **88** | **4253** | **4400** |
| **B** | | | | |
| (iii) 50 YI workers in the presence of 10 OE workers | **27** | **44** | **2729** | **2800** |
| Expected frequency | 43.33 | 43.33 | 2713.33 | |
| Chi-squared contribution | 6.156 | 0.010 | 0.090 | |
| (iv) 10 OE workers in the presence of 50 YI workers | **25** | **8** | **527** | **560** |
| Expected frequency | 8.67 | 8.67 | 542.67 | |
| Chi-squared contribution | 30.782 | 0.051 | 0.452 | |
| Total | **52** | **52** | **3256** | **3360** |
| **C** | | | | |
| (ii) 50 YI workers | **18** | **24** | **1558** | **1600** |
| Expected frequency | 16.36 | 24.73 | 1558.91 | |
| Chi-squared contribution | 0.164 | 0.021 | 0.001 | |
| (iii) 50 YI workers in the presence of 10 OE workers | **27** | **44** | **2729** | **2800** |
| Expected frequency | 28.64 | 43.27 | 2728.09 | |
| Chi-squared contribution | 0.094 | 0.012 | 0.000 | |
| Total | **45** | **68** | **4287** | **4400** |
| **D** | | | | |
| (i) 50 OI workers | **41** | **64** | **2695** | **2800** |
| Expected frequency | 55.00 | 60.00 | 2685.00 | |
| Chi-squared contribution | 3.564 | 0.267 | 0.037 | |
| (iv) 10 OE workers in the presence of 50 YI workers | **25** | **8** | **527** | **560** |
| Expected frequency | 11.00 | 12.00 | 537.00 | |
| Chi-squared contribution | 17.818 | 1.333 | 0.186 | |
| Total | **66** | **72** | **3222** | **3360** |

A: chi squared=4.150, d.f.=2, $P$=0.126.
B: chi squared=37.543, d.f.=2, $P$=0.000.
C: chi squared=0.292, d.f.=2, $P$=0.864.
D: chi squared=23.205, d.f.=2, $P$=0.000.
Bold indicates observed values, and row and column totals.