

Ant search strategies after interrupted tandem runs

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SUMMARY

Tandem runs are a form of recruitment in ants. During a tandem run, a single leader teaches one follower the route to important resources such as sources of food or better nest sites. In the present study, we investigate what tandem leaders and followers do, in the context of nest emigration, if their partner goes missing. Our experiments involved removing either leaders or followers at set points during tandem runs. Former leaders first stand still and wait for their missing follower but then most often proceed alone to the new nest site. By contrast, former followers often first engage in a Brownian search, for almost exactly the time that their former leader should have waited for them, and then former followers switch to a superdiffusive search. In this way, former followers first search their immediate neighbourhood for their lost leader before becoming ever more wide ranging so that in the absence of their former leader they can often find the new nest, re-encounter the old one or meet a new leader. We also show that followers gain useful information even from incomplete tandem runs. These observations point to the important principle that sophisticated communication behaviours may have evolved as anytime algorithms, i.e. procedures that are beneficial even if they do not run to completion.

Key words: *Temnothorax albipennis*, tandem runs, superdiffusive, search patterns, anytime algorithms.

INTRODUCTION

The search strategies of animals have long been of interest because they combine issues of information availability, information gathering and navigation skills. A classic example is Tinbergen's studies from the 1930s of nest finding by *Philanthus* wasps (Tinbergen, 1958; Tinbergen, 1972). Here the wasps' nest was static but Tinbergen could change the location of the wasps' search for it by moving learnt landmarks. Search for a stationary and permanent target may, however, be relatively easy compared with search say by a predator for prey that are mobile and unpredictable in time and space (Sims et al., 2008). So one issue is just how intensively or extensively should a seeker search. In the present study, we examine an unusual and very intriguing case in which certain potential goals will be static but are of different value and where a key target will be near and stationary for a predictable time before it moves away rapidly.

The case in point occurs during nest emigration in certain ants. When individual workers of *Temnothorax albipennis* have found a suitable new nest they return to the old nest and recruit single followers in a process called tandem running in which they teach their disciple the route to the new nest. Such tandem runs frequently break up in the hinterland between the old and new nest. The leader then waits stock-still for its lost follower for a certain amount of time before giving up and leaving the vicinity of the break-up (Richardson et al., 2007). In this case, the former follower could presumably look for its lost leader, try to return to the relative safety of the old nest or attempt to extrapolate from the direction of the aborted tandem run to have a better chance of finding the new nest.

The intensity or extensity of animal search strategies has recently attracted new attention due to an influx of ideas from physics concerning patterns of movement that can range from sub-diffusive,

through diffusive (Brownian motion) to superdiffusive (Shlesinger and Klafter, 1986; Viswanathan et al., 1996; Viswanathan et al., 1999; Bartumeus et al., 2005; Bartumeus, 2007; Bartumeus, 2009; Benhamou, 2007; Benhamou, 2008; Reynolds et al., 2007a; Reynolds et al., 2007b; Reynolds, 2009; Reynolds and Rhodes, 2009). Such studies have often looked at the search by predators for prey (Edwards et al., 2007; Travis 2007; Sims et al., 2008). To evaluate the effectiveness of such search strategies, however, much needs to be known about the distribution in space and time of prey populations. This can be exceedingly difficult. Search for static old and new homes or even single nest-mate leaders might simplify the problem, because of the restricted and small number of possible targets and their relative predictability in time and space.

Our study system is tandem running in the ant *Temnothorax albipennis*. In tandem running, one ant literally leads a single nest mate to a goal such as food or a new nest site (Möglich, 1978). The tandem leader shows the tandem follower a route. This recruitment communication is also of special interest because it was the first case in which teaching, as strictly defined (Caro and Hauser, 1992), was shown in a non-human animal (Franks and Richardson, 2006). During a tandem run, the leader's path is much less tortuous than that of the follower, who frequently turns from side-to-side and may even loop around in a complete tight circle. *Temnothorax albipennis* workers can learn landmarks (Pratt et al., 2001; McLeman et al., 2002) and probably also use path integration (Müller and Wehner, 1988) for navigation. We strongly suspect that *T. albipennis* uses tandem running rather than carrying nest mates, which is three times faster, because carried ants cannot learn the route. So, unlike a tandem follower, a carried ant does not subsequently recruit nest mates. Carried

ants cannot learn the route probably because the use of a path integrator would require them to have paced-out their path (Wittlinger et al., 2006), and the head of a carried ant is orientated upside down and backwards, which probably precludes it from learning landmarks (Pratt et al., 2002). The benefit of tandem running, even though it is slow, is that followers can become, in turn, leaders (Möglich, 1978). So tandems serve to recruit recruiters and initiate a cascade of useful information through members of the ant colony. Tandem runs are slow because the leader frequently waits for the follower to catch up. The follower then taps with her antennae on the gaster and hind legs of the leader to signal that the tandem should continue. There is feedback in both directions between the leader and the follower and the leader adjusts how long it waits for lost followers before 'giving up', depending on (1) how much they have invested in the tandem so far, (2) the rate at which the tandem has proceeded, and (3) the quality of the goal (Richardson et al., 2007). For all of these reasons, it is clear that tandem running in ants is a remarkably sophisticated behaviour, although one that is probably based on a few simple rules.

We ask what tandem leaders do, within the context of new nest site selection during colony emigration, when they finally give up on a lost follower and equally importantly what can tandem followers gain from incomplete tandem runs that do not arrive at the goal? It seems plausible that a follower that has lost its leader could use the knowledge it had gained from following the tandem run to return to the old nest. After all, this is often what happens after a complete tandem run has arrived at the new nest. Alternatively, a follower might start searching from the point at which the tandem broke up. Homeward bound, but displaced, desert ants (Wehner and Srinivasan, 1981; Müller and Wehner, 1994; Wehner et al., 2002) and similarly displaced honeybees (Reynolds et al., 2007a) search around the area where they 'expect' their nest or hive to be and it has been argued that they might search in spirals (Müller and Wehner, 1994) or with the characteristics of superdiffusive Lévy flights [i.e. random walks where the step lengths are derived from power-law distributions such that many of the steps are short but some are very long indeed (Reynolds et al., 2007a) (see also Fourcassié et al., 1992)] or even initially in Lévy loops [i.e. where the lengths of the loops are derived from power-law distributions (Reynolds, 2008)]. However, nest sites and hives do not move whereas a lost leader will eventually leave (Richardson et al., 2007), so the search patterns of tandem followers who have lost their leader are of special interest. Indeed, in terms of searching for an ephemeral target they may face a similar problem to honeybees looking for new food sources in the vicinity of those that have become exhausted (Reynolds et al., 2007b). We also explore the extent to which such searchers can use information obtained from guidance by their former tandem leader to extrapolate beyond the aborted tandem run.

MATERIALS AND METHODS

Sample collection and colonies

Thirteen colonies of *Temnothorax albipennis* (Curtis) were collected on the 29 September 2007 from Dorset, England, UK. Experiments were run between 13:00 h and 17:30 h four days a week from mid-October to mid-December 2007. Each colony was housed in a nest made from a cardboard gasket set between two glass slides, creating a cavity with internal dimensions 50 mm × 35 mm × 1.5 mm and a 2 mm wide entrance. The colonies were provided weekly with *Drosophila*, dilute honey solution and water.

Experimental procedures

We carried out three experiments. Experiment 1 examined what tandem leaders do when they depart after 'giving up' on a removed follower. Experiment 2 tested whether the duration of the tandem run before interruption (by removal of the follower) influenced the leader's behaviour. Experiment 3 examined the search behaviour of a former follower after its leader had been removed.

For each run of experiments 1, 2 and 3, a colony was placed in the centre of the arena so that the entrance was randomly orientated 'North, South, East or West' in experiment 1 or 'North or South' in experiments 2 and 3. Each emigration was induced by removing the top microscope slide from the old nest. To interrupt tandem runs either the follower, in experiments 1 and 2, or the leader, in experiment 3, was removed with a fine brush. We performed this operation during one of the frequent and naturally occurring gaps between the follower and leader, so that the remaining member of the pair was not disturbed. Manipulated tandem members were isolated from their nest mates until the end of the tandem running period, when the experiment was terminated. Colonies were left for at least one week after each experiment, to prevent any influence of learning that occurs during emigrations (Langridge et al., 2004). Only forward tandem runs were used in all three experiments.

Once the leader had abandoned the removed follower [defined by the leader moving 1 cm away from the interruption point (IP)], or the leader was removed, the remaining focal ant was observed for a maximum of 5 min. To prevent further interaction between the focal ant and nest mates, all other ants were redirected with a fine paint brush so that they could neither contact the leader during its waiting period nor approach the follower. In experiments 1 and 2, we simply observed what leaders that had given up on their lost follower did next, e.g. visiting one of the nests. In experiment 3, we videotaped both the tandem run and the subsequent behaviour of the follower for 5 min after the leader had been removed.

Experiment 1: tandem leaders after giving up

The emigration arena consisted of four peripheral arenas around a central one (all 23 cm × 23 cm Petri dishes, Fig. 1). This setup was similar to that used by Richardson et al. (Richardson et al., 2007). The peripheral arenas each contained new equal-quality nests of a higher standard than the original, as determined experimentally by Franks et al. (Franks et al., 2003). Specifically, the nests were 50 mm × 35 mm × 1.5 mm, dark (i.e. with a red filter ceiling) and with a 2 mm entrance. Each bridge between these large Petri dishes was formed by a small Petri dish, atop its lid, and acetate ramps. This arrangement ensured the ants made enough tandem runs before the switch to social carrying. Graph paper inscribed with rings to form a radiating series of 2 cm bands was placed under the arena to track the spatial positions of ants.

After an emigration had begun and forward tandem runs headed towards one of the four new nests, the follower in a tandem pair was removed at an 'IP' on one of the bridges, halfway between the old and new nests. A total of 37 tandem runs, from five colonies, were interrupted and each leader's behaviour was monitored by eye and assigned to certain categories.

Experiment 2: tandem leader behaviour with varying investment
The emigration arena (82 cm × 53 cm) contained two equal-quality new nests of a higher standard than the old nest (cavity, 50 mm × 35 mm × 1.5 mm, made dark with black card and with a 2 mm-wide entrance, Fig. 2). Two new nests were placed, equidistantly from the central old nest, so that they were opposite one another.

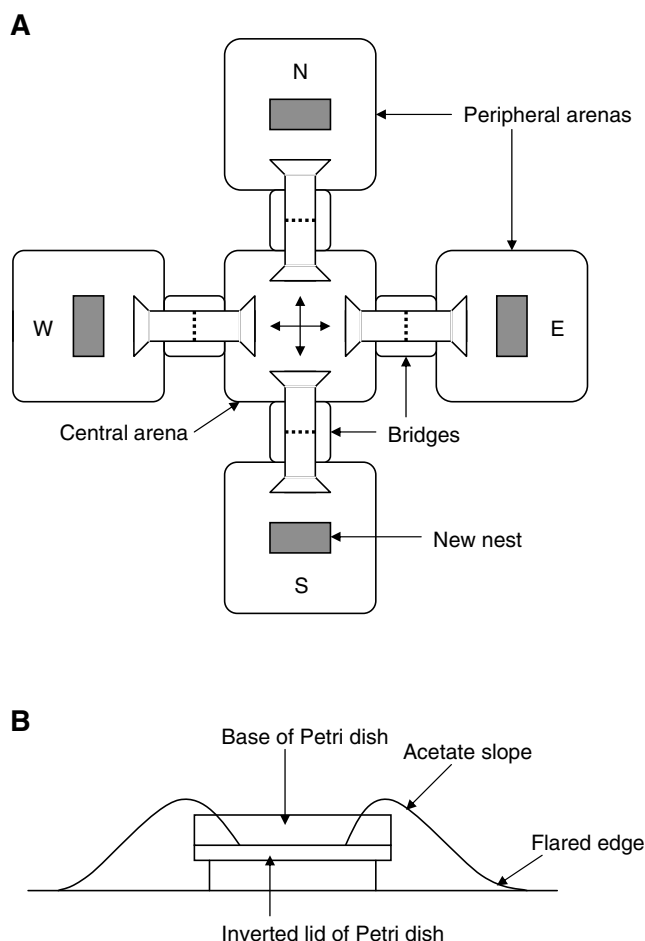


Fig. 1. (A) Experiment 1 – plan view of emigration arena, which consisted of five large Petri dishes (23 cm × 23 cm) linked by four smaller Petri dishes (10 cm × 10 cm). The cross of arrows indicates where the old nest was placed centrally with its entrance in a randomised orientation. The broken lines mark the halfway interruption point for tandem runs along the bridges. (B) Cross-section of one of the bridges. The inverted lid has grooves cut into its walls to slot over the arena walls. The flat surface in the middle of the acetate slope facilitated removing the tandem follower without disturbing the leader. N, North, E, East, S, South, W, West.

Each new nest lay within a small Petri dish (10 cm × 10 cm) that had a 1.5 cm gap cut into its side (Fig. 2). This reduced the discovery rate of the target nest sites, so that the tandem-running stage of colony emigration ('deliberation' period) was extended, and more tandems were formed. The Petri dishes were temporarily removed if the searching follower approached the dish's edge, so the free-roaming nature of the path would not be compromised by edge following. Graph paper with a 2 cm × 2 cm coordinate grid (and a radiating series of 2 cm bands, as in experiment 1) was placed under the arena to indicate the spatial position of the ants within the arena.

Once a tandem run began, the follower was removed at one of three randomly alternated distances. Interruption point 1 (IP1), interruption point 2 (IP2) and interruption point 3 (IP3) were, respectively, at a $\frac{1}{2}$, $\frac{1}{4}$ or $\frac{3}{4}$ of the way to each new nest. The IP was randomly pre-determined. The three IPs either side of the old nest were designated by lines on the graph paper beneath the arena. A total of 25 repeats for each IP were collected using 10 colonies, and each leader's activity was monitored by two observers and its behaviour was categorised.

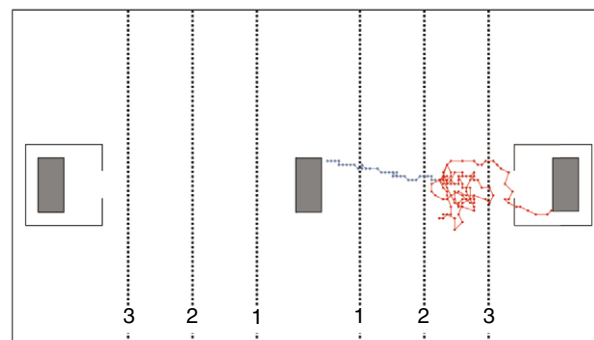


Fig. 2. Experiments 2 and 3 – plan view of the (82 cm × 53 cm) emigration arena, with the two alternative 'East' and 'West' nest sites. The old nest was placed in the centre of the arena. The broken lines mark interruption points 1, 2 and 3 (IP1, IP2 and IP3, respectively) in both directions towards either of the two new nests. The small Petri dishes had 1.5 cm entrances cut into one of their walls. In experiment 3, the small Petri dishes were turned upside down to cover the new nests. Also shown is an example of the path taken by a tandem pair (blue line and circles) and then the follower after interruption (red line and circles). The tandem run headed 'East' and was interrupted at IP2. The follower (number 18) appears to perform a diffusive search before finding the new nest.

Experiment 3: former tandem followers

The same emigration arena was used as in experiment 2. However, the two Petri dishes with a single 1.5-cm entrance hole orientated towards the old nest were inverted and placed over the target nests. This extended the tandem-running stage even further. Graph paper inscribed with a 0.5 cm × 0.5 cm coordinate grid was placed under the arena to indicate the spatial position of the ants.

The leader, of a tandem run, was removed at one of the three IPs as in experiment 2. The IP being randomly selected *a priori*. The paths of both the tandem and the post-interruption follower were recorded using a high-definition video camera [Sony FX1 (Tokyo, Japan) streaming directly to a PC]. The ant's position, i.e. the coordinates of its head, was recorded at intervals of 1 s. We recorded the follower for the entire 5-min period or until it found the old or new nest. A total of 13 replicates for each IP were collected using six colonies.

For every 1 s time step the heading for both tandems and followers were measured from the absolute 'East' or 'West' heading, depending upon which nest the tandem was travelling towards (Fig. 2). The mean compass headings (0–360 deg.) of tandems and former followers were calculated with circular statistics (Batschelet, 1981) using the package Oriana, version 1.06 (1994, Warren L. Kovach, Kovach Computing Services, Pentraeth, Wales, UK). This form of averaging ensured that the mean compass heading was influenced predominantly by the orientation of the majority of individual steps, rather than the final destination. For example, a former follower that continued to move towards the new nest (0 deg.) for the majority of its total path, but later made a straight run back to the old nest (180 deg.), would still receive a mean heading of approximately 0 deg.

Trajectory analysis and statistical methods for experiment 3

We applied multi-linear regression to find out whether there was any behavioural transition in the search by the former follower in each tandem run. For each IP we pooled the displacement distributions based on the crossovers, between initial/final search phases, estimated with the multi-linear regression. We used the

'segmented' R-package to compute multi-linear regression lines on the log-binned root mean square (r.m.s.) displacement plots. The log-binning allowed us to obtain better regression estimates of the slopes.

The re-sampling of former followers' paths, each of them now divided into initial and final search phases, was carried out according to the 'local' method for connecting points representing changes in direction of more than 90 deg. (Reynolds et al., 2007a) (Fig. 3). Applying Bartumeus and Levin's point-wise selection method (Bartumeus and Levin, 2008), we observed that at the threshold angle of 90 deg., a uniform distribution was selected against an exponentially decaying distribution. The choice of 90 deg. was further justified by analyses of the effect of varying the threshold angle, which showed that the patterns observed for the flight length distributions strengthen at 110 deg. and disappear at 60 deg., suggesting that 90 deg. is an adequate threshold angle. Therefore, for the flight representation we used only those points from the original raw data paths for which the direction of movement changed more than 90 deg. compared with the direction of movement of the previous point.

We focus our interest on the behaviour of the 'tail' of the displacement distributions, which govern the long/mid-term diffusive properties of movement. With that aim, we performed sequential point-wise model comparisons (SPWMC) based on Akaike's Information Criterion (AIC). The comparison is established by computing the Akaike weights (wAIC) and the relative likelihood of each model compared with the likelihood of the best-fit model (AIC_{\min}). The wAIC-based SPWMC analysis

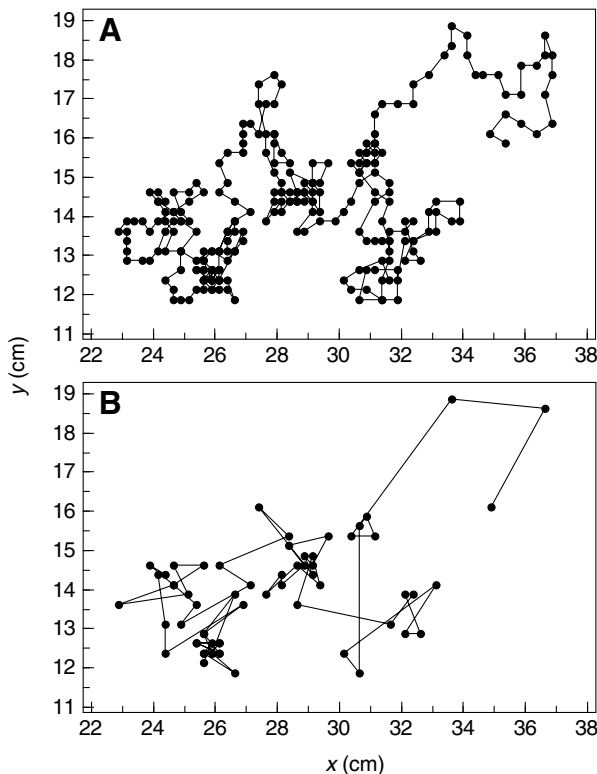


Fig. 3. (A) An example of a raw path (for the follower in tandem 8). (B) The path in A is re-sampled into flights between points where a change in direction of more than 90 deg. has occurred, according to the 'local' procedure in Reynolds et al. (Reynolds et al., 2007a). See text for further details.

(Bartumeus et al., 2010) facilitates a comparison of the fits of different probabilistic models on different regimes of a given empirical distribution, and provides more statistical power than other methods suggested in the literature in particular when dealing with small datasets. In this paper, our goal, rather than look for 'the very best' fit for the tail of the wAIC-based SPWMC analysis, is to determine how near, or far away, are the 'tails' of the displacement distributions from two limiting-case models: the exponential and the truncated power-law model (see Appendix for mathematical expressions for models). On the one hand, exponential displacement distributions involve normal diffusion at a macroscopic level whereas on the other hand truncated power-law displacement distributions hold superdiffusive properties over a wide range of scales, given that the convergence to normal diffusion is ultra slow. We performed indirect (i.e. goodness-of-fit) and direct (i.e. likelihood ratio) 'tail' tests (i.e. for the 70% percentile) comparing the exponential and the truncated power-law models in each empirical distribution (see Appendix). The goodness-of-fit tests are based on the Kolmogorov–Smirnov (KS) statistic and are obtained from 2500 Monte Carlo (MC) replicates (Clauset et al., 2009) (see Appendix). The P -values associated with these goodness-of-fit tests indicate how likely it is that the data comes from a given model and tell us whether the chosen models are (statistically) good representations of the data (P -value > 0.1) or not (P -value < 0.1). The likelihood ratio tests and the associated P -values are computed as in Clauset et al. (Clauset et al., 2009). Importantly, both the goodness-of-fit tests and the likelihood ratio tests illustrate how close the empirical 'tails' are to the two limiting-cases rather than assuming that one model or the other is 'the very best' fit. Finally, we allow for visual validation of the compared models by plotting the two model fits (i.e. exponential and truncated power law) with the corresponding cumulative distribution functions. These plots are meant only to show the qualitative behaviour of the distributions and the fits, i.e. they are not used to estimate the parameters of the distributions. Instead, we obtain maximum likelihood estimates of the probabilistic models used by numerically maximising the appropriate log-likelihood functions, and we compute 95% confidence intervals (CI) using the likelihood ratio test (Edwards et al., 2007; Clauset et al., 2009; Bolker, 2008). All the statistical computations are performed using R, version 2.2.0 (<http://www.r-project.org>) and the 'bbmle' R-package made available by B. Bolker (<http://www.zoology.ufl.edu/bolker/>) (see also Bolker, 2008).

Spatial simulations of follower searches were carried out in NetLogo (<http://ccl.northwestern.edu/netlogo/>).

RESULTS

Experiment 1: tandem leaders after giving up

After giving up on their removed follower, 92% of tandem leaders proceeded to the new nest towards which they had been heading ($N=37$). The only other behaviours observed were one return to the old nest and two cases that were indeterminate.

Experiment 2: tandem leader behaviour with varying investment

After giving up on their follower, 72% of the leaders arrived at one of the two new nests (i.e. 54 out of the total of 75 ants, Table 1). The number of ants arriving at the new nests or performing other behaviours did not differ statistically between IP1, IP2 and IP3 ($\chi^2=0.397$, d.f.=2, $P<0.820$). Twelve per cent of the leaders recruited a new ant, from the area between the nests, after giving up on their former follower ($N=9$) and one ant became a reverse tandem follower.

Table 1. Leader behaviour after giving up on former followers at interruption points 1, 2 and 3

Leader behaviour	Observed frequencies at interruption point			Total
	1	2	3	
Entered new nest	18	17	19	54
Other behaviour	7	8	6	21
Total	25	25	25	75

The expected frequency was 18 for each case of 'entered new nest' and 7 for each case of 'other behaviour'.

Experiment 3: former tandem followers

After interruption, many of the 39 former followers eventually found the old nest (53%, $N=21$) or the new one (21%, $N=8$, Table 2, Fig. 4). The remaining ants continued searching for the full 5 min (26%, $N=10$). The numbers of ants performing each behaviour were different from those expected by chance at each IP ($\chi^2=9.91$, d.f.=2, $P=0.007$). The number of ants that eventually found the old nest decreased across IP1, IP2 and IP3 whereas those finding the new nest or continuing with a fruitless search increased.

For the majority of the former followers' paths, steps were predominantly in the direction they had been led during the aborted tandem run (Fig. 5). From IP1 to IP3, the accuracy of follower orientation increased (absolute difference from 0 deg. decreased), as did the precision (increase in vector length, decrease in variance, Table 3).

We explored whether there was any behavioural transition in the search of former followers by testing whether there were changes in their diffusive (spreading) properties over time. By later re-sampling the paths into flights we explored whether the observed changes in the diffusivity might be explained by changes in flight length distributions.

Our earlier work (Richardson et al., 2007) has shown that tandem leaders deprived of their follower remain in a stationary wait for longer the greater the duration of the tandem run up to the point when the follower lost contact. This relationship can be described as mean $\log_{10}(\text{leader abandon time})=0.9651+0.3895\log_{10}(\text{tandem duration})$ ($R^2=0.99$; $P<0.001$). (These data are from a total of 184 tandem runs interrupted at six different points.) Given that tandem followers can become tandem leaders on the next run, it seems reasonable to suppose that they will be equipped with the same algorithms and should therefore be able to estimate how long their lost leader should wait for them.

Leaders might be expected to wait for 35.76 s (95% CI: 32.38–38.70), 48.28 s (95% CI: 45.12–51.14) and 59.69 s (95% CI: 55.76–63.25) at IP1, IP2 and IP3, respectively. We term these leader

Table 2. The behaviour of former tandem run followers at interruption points 1, 2 and 3

Follower behaviour	Observed frequencies at interruption point			Total
	1	2	3	
Entered old nest	11	7	3	21
Other behaviour	2 (1)	6 (2)	10 (5)	18 (8)
Total	13	13	13	39

The expected frequency was 7 for each case of 'entered old nest' and 6 for each case of 'other behaviour' (includes both finding the new nest and finding neither nest during the first five minutes after the leader was removed). The numbers in parentheses represent the ants that found the new nest.

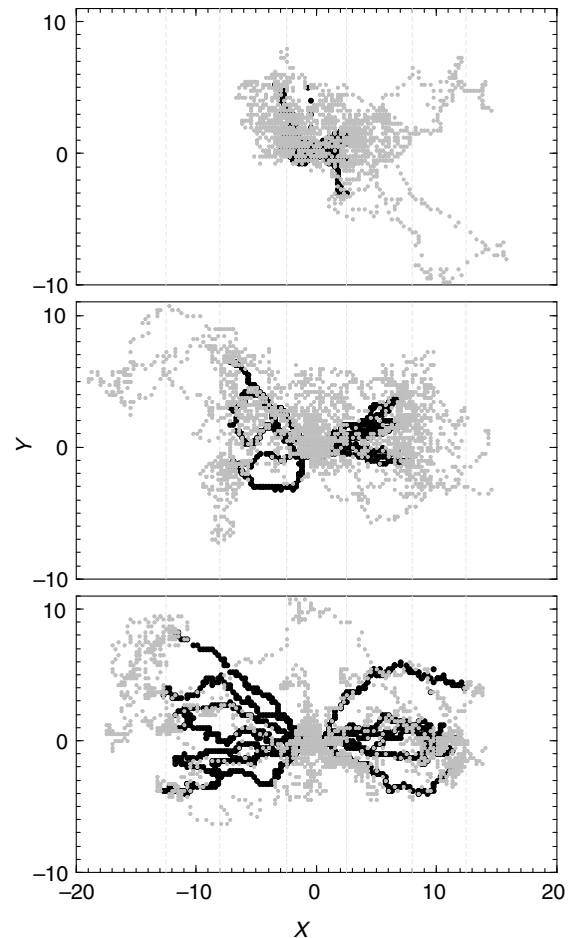


Fig. 4. Raw paths for interruption points 1, 2 and 3, respectively, normalised so that they all originate in the centre of the arena. Black symbols are the coordinates of the tandem runs; grey symbols are the paths of the former followers after their tandem leaders have been removed.

giving-up times (LGUTs). Most intriguingly, the crossover value estimated by the multi-linear regression model, fitted to the r.m.s. displacement for the pooled paths of all former followers for each IP, matches very closely the LGUT for that point (Fig. 6). The crossover values are 37.15 s (95% CI: 18–75), 47.86 s (95% CI: 34–68) and 50.93 s (95% CI: 34–75, Fig. 6). This strongly suggests that former followers change their search behaviour according to the time their lost leader is likely to have attempted to wait for them.

Indeed, when we split the search flights into two stages, before and after LGUT, we find that the exponents for each stage are significantly different for IP2 and IP3 but not for IP1 (Fig. 6). So compared with a follower that only has a brief 'lesson' a follower that participates for longer will spend longer in the local area before making the transition to 'superdiffusive' movement. Follower's searching behaviour 'before' the leader is expected to abandon is diffusive (not significantly different to the exponent of a Brownian walker, i.e. 0.5) at IP1 and IP3. For IP2 there is even a possibility of sub-diffusion (slower spreading and more re-sampling than a Brownian walker would exhibit, i.e. <0.5). However, 'after' the leader is expected to have left the locality, the follower's movement is significantly different to that of a Brownian walker (exponent >0.5), so over time follower movement makes a transition from 'diffusive or sub-diffusive' to 'superdiffusive' movement, and

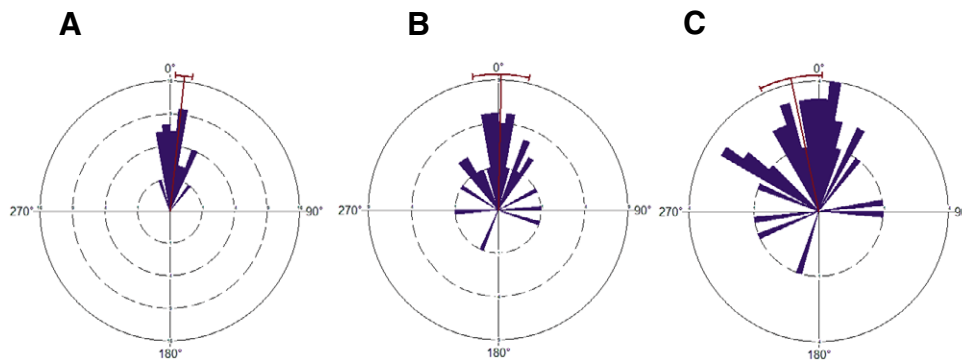


Fig. 5. Path vectors (compass headings) for (A) all tandems and (B) former followers. Each path was reduced to a single mean compass heading. Wedge area is proportional to frequency. The new nest was at 0 deg., the old nest was at 180 deg. Watson's F -tests for two circular means $F=0.53$, $d.f.=76$, $P=0.47$. See Table 3 for circular statistics split according to interruption point (IP). (C) Difference between paired compass headings for former followers and their tandems. We subtracted the mean compass heading for each former follower from that for its tandem. Then we converted all differences to angles of up to 180 deg. Finally we placed all differences where the former follower had the greater mean compass heading to the left of 0 deg. (360 deg. – difference) and all differences where the tandem had the greater mean compass heading to the right of 0 deg. (0 deg. + difference). The resulting distribution has a sample mean vector of 347.99 deg. with a 95% CI of 1.60 deg. to 334.39 deg. and is significantly different from uniform (Rayleigh test for uniformity, $P<0.01$). This means the paired compass headings do not differ significantly. All calculations were carried out in Oriana, version 1.06, 1994; Warren L. Kovach, Kovach Computing Services, Pentraeth, Wales, UK). The red lines indicate the mean compass heading and its 95% CI. The mean is denoted by the red radius, the 95% CI is denoted by the red interval round part of the circle. CI, confidence interval.

the timing of this transition appears to be later with increasing tandem duration (Fig. 6).

After re-sampling of the paths into flights (Fig. 3), it is clear that the flight direction distributions are uniform (Fig. 7).

The SPWMC suggests that from IP1 to IP2 and IP3 the change from a diffusive to a superdiffusive search is related to a change in the distribution of flight lengths from exponential to power law. The search behaviour of the former follower before the leader should have walked away (Fig. 8A) shows that as the number of points included from the tail increases (from right to left) the distribution of flight lengths for the three IPs quickly converges to a truncated exponential. IP3 approaches a truncated exponential a bit slowly but the test is noisy [it only approaches a truncated power law (TPL) intermittently in three tail 'sizes']. Overall, the separation between IP1, IP2 and IP3 is minimal. The search behaviour of the former follower after the leader should have walked away (Fig. 8B) shows overall a very clear separation between IP1, IP2 and IP3. IP1 quickly and clearly converges to a truncated exponential. IP2 requires the inclusion of more points from the tail to converge to a truncated exponential after getting quite close to a TPL. Finally, although IP3 eventually converges to a truncated exponential it hovers close to a TPL over quite a range of inclusivity of data points from the tail. So in general this analysis suggests that at IP1 the search by the former follower approximates Brownian movement both before and after its original leader should have walked away but at IP2 and

IP3 it appears that the search may switch from Brownian-type flight lengths to those from a TPL at the point at which the former tandem leaders should have walked away.

This interpretation is consistent with the indirect (i.e. goodness-of-fit) and direct (i.e. likelihood ratio) tests comparing the exponential and the truncated power-law models for the 70% percentile tails in each empirical distribution (Table 4). Before the LGUT, the search of the follower at IP1 is such that the distribution of flight lengths is compatible with both a TPL and an exponential distribution model (compare MC P -values). However, the exponent for the TPL is roughly 3; hence, either way the evidence points towards Brownian motion. The search of followers at IP2 and IP3 combined is performed with flight lengths that are not compatible with a TPL but are compatible with an exponential distribution (compare MC P -values). This picture is also confirmed by the wAICc and the sign of the likelihood ratio (LR), even though the LR is not significant (LR P -value >0.1). In any case, these data also seem to be compatible with Brownian motion. After the LGUT, the search of the follower at IP1 is such that the data are not compatible with a TPL but they are compatible with an exponential distribution (compare MC P -values), although neither model fits better than the other (the wAICcs show more weight of evidence for the exponential model but LR P -value >0.1). Hence, in general for IP1 there is no evidence for superdiffusion either before or after the LGUT. However, the search of followers at IP2 and IP3 (combined) after the LGUT, is such that

Table 3. Circular statistics for tandems and former followers

	Interruption point	Mean compass heading (deg.)	Length of compass heading vector	Circular variance	Circular s.d.	s.e.m.
Tandems	1	8.46	0.98	0.02	12.05	3.78
	2	7.00	0.98	0.02	12.32	3.86
	3	2.22	0.99	0.01	7.45	2.34
Former followers	1	353.23	0.60	0.40	58.16	17.40
	2	7.44	0.95	0.05	18.96	5.95
	3	359.42	0.85	0.15	32.11	10.03

As the mean compass heading is a vector not a scalar measurement, it has a corresponding length dimension, which reflects the overall degree of scatter, calculated in Oriana, version 1.06, 1994, Warren L. Kovach, Kovach Computing Services, Pentraeth, Wales, UK.

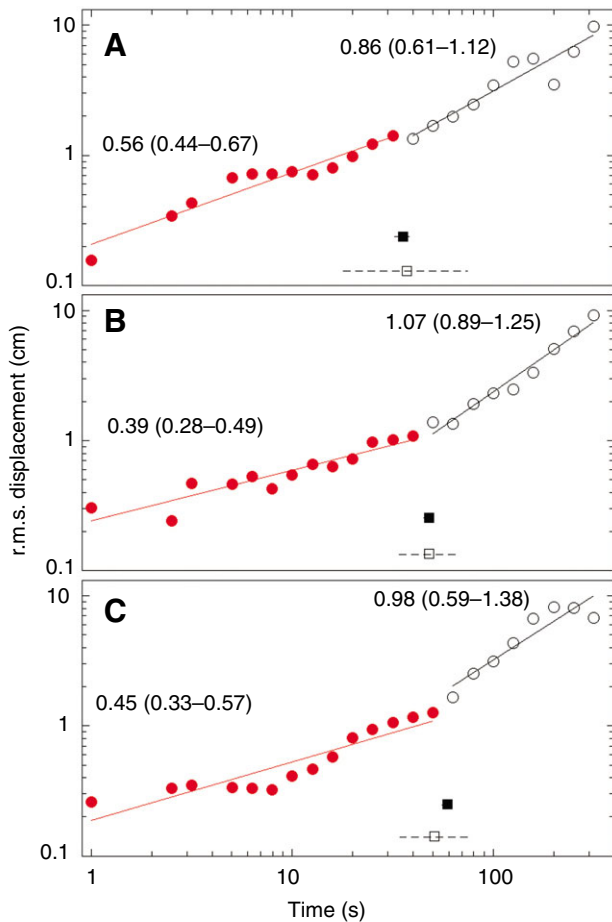


Fig. 6. Log-binned root mean square (r.m.s.) displacement for the search process of former followers as a function of the time since their leader was removed. For each tandem, we calculated the squared displacement of the follower as a function of the time since the leader was removed. We then averaged across tandems to calculate the mean net squared displacement and then took the square root to obtain the r.m.s. displacement as a function of time. Times were binned logarithmically to improve the reliability of the means at long times and the overall regression analyses. The data for all former followers have been pooled for each of the interruption points (A) 1 (IP1), (B) 2 (IP2) and (C) 3 (IP3). A leader might have been expected to remain stationary for 35.76 s (95% CI: 32.38–38.70), 48.28 s (95% CI: 45.12–51.14) and 59.69 s (95% CI: 55.76–63.25), before leaving the vicinity of IP1, IP2 or IP3, respectively (Richardson et al., 2007). These expected 'leader giving-up times' (LGUTs) are represented by filled squares (mean) and solid lines ($\pm 95\%$ CI). Those estimated from the actual r.m.s. curves are IP1, 37.15 s (95% CI: 18–75), IP2, 47.86 s (95% CI: 34–68) and IP3, 50.93 s (95% CI: 34–75). These r.m.s. breakpoints are represented by empty squares (mean) and broken lines ($\pm 95\%$ CI). The slopes of the six regression lines and their 95% CI are shown. IP1, before, $F_{1,10}=118.03$, $P<0.0001$, $R^2=91.4\%$; IP1, after, $F_{1,8}=62.16$, $P<0.0001$, $R^2=87.2\%$; IP2, before, $F_{1,11}=66.39$, $P<0.0001$, $R^2=84.5\%$; IP2, after, $F_{1,7}=189.65$, $P<0.0001$, $R^2=95.9\%$; IP3, before, $F_{1,12}=65.59$, $P<0.0001$, $R^2=83.2\%$; IP3, after, $F_{1,6}=37.77$, $P=0.001$, $R^2=84.0\%$. Although the logarithmic binning accounts for a better estimation of the slopes and the crossovers, the results hold qualitatively without binning the data.

the flight length distribution is compatible with both a TPL and an exponential but are more compatible with the former (compare MC P -values). Furthermore, the wAICc shows more weight of evidence for the TPL model, and there is some evidence from the LR test that TPL fits better than exponential (LR P -value=0.1). The exponent for the TPL is <3.00 . Hence, overall the combined data for IP2 and IP3

suggest that the change in the movements of former followers from diffusive to superdiffusive after the LGUT (Fig. 6) is due, at least in part, to a change from an homogeneous (i.e. exponential-like) to a much more right skewed and heterogeneous (i.e. power-law-like) flight length distribution (Fig. 8; Table 4).

Qualitatively the above results are validated by the visual inspection of the shape of the survivorship plots for the flight distributions (Fig. 9). It is clear that for IP1 the exponential and TPL fit equally well the survival function for the former follower searches for both before and after the leader is likely to give up waiting. By contrast, for the combined IP2 and IP3 data, while the survival function for the former follower search before the LGUT is fitted better by the exponential model, the survival function for the former follower search after the LGUT is fitted better by the TPL model (Fig. 9).

We have also explored the potential abilities of followers to reunite with their lost leaders through computer simulations based on the empirical flight length distributions. For a population of searching followers, the cumulative proportion that successfully reconnected to their leader quickly reaches a plateau: the first few flights are crucial. The greater the disparity between the leader's and the follower's body orientations at the start of the search, the lower the probability of reconnecting. If the leader remains stationary, or goes very slowly, the probability of the follower successfully reconnecting is far higher (Figs 10 and 11).

Hence, the transitions we observe between initial diffusive searchers to more superdiffusive searches with the switches occurring at the point that the former leader is likely to have walked away make sense because lost leaders are initially likely to be close by and might best be sought by a more local search but when eventually they give up on their lost follower, such followers might then do well to engage in a superdiffusive search for an alternative leader, or the safety of the old or the new nest. Our analysis also suggests that the superdiffusive properties might be partially explained because of a change in the flight length distribution (the distribution of directionally correlated displacements occurring between strong turns) from exponential-like to power-law-like behaviour. The benefits of an initial local search are shown by the results of our simulations (Figs 10 and 11). The probability of a reconnection between a follower and a leader increases with their detection distance but decreases rapidly with time, especially if the leader leaves the scene swiftly.

DISCUSSION

When tandem runs are interrupted through the removal of the follower, leaders first remain stationary and then, in the vast majority of cases, they proceed directly to the new nest (summing across experiments 1 and 2, 79% of former leaders went directly to the new nest). In the context of house hunting, this behaviour might be strategically beneficial because a leader, once it has given up on its lost follower, could rapidly determine if a quorum has been met in the new nest site and might then switch from slow tandem running to carrying of nest mates, which is three times quicker (Pratt et al., 2002). Such behaviour might also be tactically beneficial because if the leader was to seek actively its lost follower by performing a looping search it might corrupt its path integrator and this might make finding the new nest much harder. The path integrators of ants are especially prone to increasing error after sharp turns (Müller and Wehner, 1988). So by waiting stock-still initially, the leader might both increase the probability of reconnection with its lost follower and minimise navigational errors so that it can continue to the new nest.

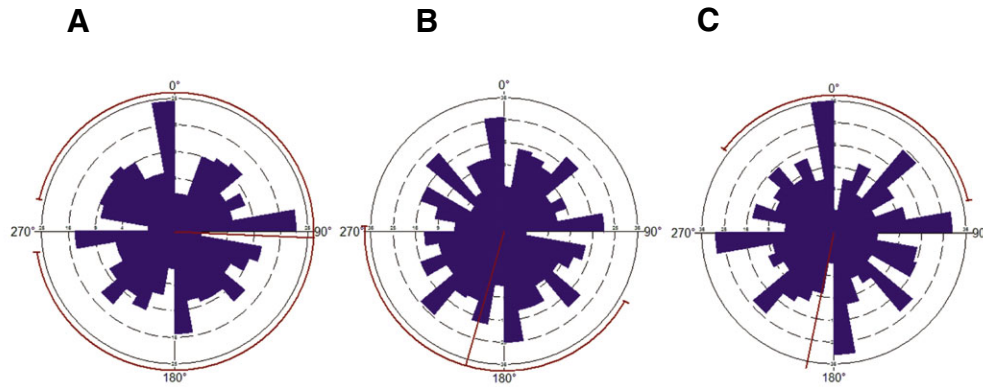


Fig. 7. Flight direction distributions for followers in tandems interrupted at: (A) interruption point 1 (IP1), (B) interruption point 2 (IP2) and (C) interruption point 3 (IP3). Each is compatible with a uniform distribution [Rayleigh test for uniformity (Batschelet, 1981), $P=0.80$, $P=0.34$, $P=0.90$ for IP1, IP2 and IP3, respectively, calculated in Oriana, version 1.06, 1994; Warren L. Kovach, Kovach Computing Services, Pentraeth, Wales, UK]. Wedge area is proportional to frequency. The new nest was at 0 deg., the old nest was at 180 deg. The red lines indicate the mean flight direction and its 95% CI. The mean is denoted by the red radius, the 95% CI is denoted by the red interval round part of the circle. CI, confidence interval.

When tandem runs are interrupted through the removal of the leader, followers often find the old or the new nest. They were more likely to find the new nest if they lost their leader closer to the new nest than the old one and *vice versa* (Table 2). The overall directions taken by former followers are influenced by the general directions of the tandem runs they had followed. Our results suggest that followers may accumulate sufficient directional information from incomplete tandem runs roughly to extrapolate their path forwards towards the possible goal. Thus, the precision and accuracy of the paths of former followers increased as a function of the duration of the tandem run. This is suggested by the increasing length of the follower's mean compass heading (a vector rather than a scalar quantity) and the decreasing absolute difference in the mean compass heading from 0 deg. (Table 3 and Fig. 5). The orientational accuracy of the tandem runs, we interrupted, was greater than that of the paths of former tandem followers after their leaders had been removed (Table 3). This is not surprising because each leader is likely to have visited the

goal, possibly several times (Mallon and Franks, 2000), before it initiated the tandem run and should only have engaged in such a costly activity if and when it had valuable information to pass on (Franks and Richardson, 2006). Moreover, tandem followers return independently from the target back to the nest, and they do not retrace the exact path of the tandem run (T.O.R., unpublished data). So it is likely that tandem followers accumulate directional information about their heading, *en route*, by using path integration or by learning fairly distant landmarks (Collett and Graham, 2004; Pratt et al., 2001; McLeman et al., 2002).

Such extrapolation beyond the tandem run by former tandem run followers is intriguingly similar to the behaviour of certain honeybees. For example, on the horizontal surface of the combs of the Asian dwarf honeybee *Apis florea*, a dancing bee can lead dance followers in a straight run aimed directly at the foraging target (von Frisch and Lindauer, 1956; Dyer, 1985). In these bees, a recruited worker, in a sense, simply extrapolates from the direction of the dance to the direction of the flight it will need to make to reach the goal.

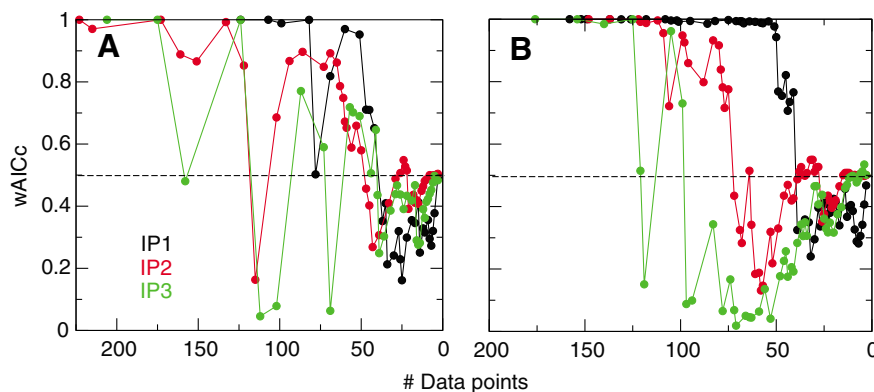


Fig. 8. Sequential point-wise model comparison (SPWMC) contrasting a truncated exponential *versus* a truncated power-law model for the flight length distributions of the three different interruption points (i.e. IP1, IP2, IP3), both at the 'initial' (A) and the 'final' (B) former follower search stages. In both models, the truncation corresponds to the maximum flight length observed. Considering truncated models accounts for a more conservative analysis where the limiting tail behaviour of both models converge ($wAICc=0.5$), being explicitly limited by empirical observation. Initial and final search phases are estimated by multi-linear regression models fitted on individual net-square displacement plots and correspond to the period before and after 'leader giving-up time' (LGUT), respectively (see Fig. 6). In the y-axis, $wAICc$ stands for Akaike Information Criteria weights with correction for small samples. In this plot, a value of $wAICc=1$ gives the maximum weight of evidence in favour of the exponential model and $wAICc=0$ gives maximum weight of evidence to the power-law model. A $wAICc=0.5$ divides the area of selection of one model against the other (broken line). Flight length data sets are arranged in ascending order. The x-axis shows the number of points included in each of the point-wise maximum likelihood tests, from left to right we go from all the flight lengths observed to the largest ones.

Table 4. Maximum likelihood estimation of parameters for the truncated power law and the exponential 'tail' models (70% percentile tails in the empirical flight distributions) for the movements of former followers

Interruption point	Truncated power-law distribution			Exponential distribution			<i>N</i> -tail	<i>N</i>	Cut-off (cm)	LR	LR <i>P</i>
	μ (95% CI)	MC <i>P</i>	wAICc	α (95% CI)	MC <i>P</i>	wAICc					
1 before	3.43 (2.63–4.34)	0.270	0.925	1.33 (0.97–1.78)	0.395	0.074	42	138	1.23	2.52	0.39
1 after	3.21 (2.46–4.03)	0.012	0.298	0.74 (0.55–0.97)	0.512	0.702	50	167	2.30	−0.85	0.69
2 and 3 before	2.69 (2.35–3.05)	0.001	0.068	1.13 (0.97–1.32)	0.132	0.931	159	518	1.06	−2.60	0.49
2 and 3 after	2.21 (1.79–2.65)	0.786	0.984	0.58 (0.48–0.70)	0.353	0.015	114	366	1.82	4.18	0.10

We show Akaike Information Criteria weights corrected for small sample size (wAICc), Kolmogorov–Smirnov goodness-of-fit tests and likelihood ratio (LR) tests comparing the truncated power law and the exponential fits. For more details, please see Materials and methods. Before, after, before or after the leader giving-up time (LGUT), respectively; α , μ , parameters for the exponential and the truncated power law distribution, respectively; CI, confidence interval; Monte Carlo (MC) *P*, *P*-value for the Kolmogorov–Smirnov D statistic based on 2500 MC replicates (Clauset et al., 2009), wAICc could take values between 0 and 1, the latter representing the maximum weight of evidence for a given model; LR, statistic from the likelihood ratio test; and LR *P*, the associated *P*-value, computed as in Clauset et al. (Clauset et al., 2009), positive values for LR indicate that the truncated power law is better than the exponential. The values in bold indicate the maximum likelihood estimates and 95% confidence intervals for the parameters of the fitted truncated power-law and exponential distribution models, μ and α , respectively.

Former followers seem initially to exhibit a simple diffusive Brownian search (Figs 6 and 8) for their lost leader. They appear to do so for a time period that depends with remarkable precision on how long the tandem run had proceeded before it was interrupted (Fig. 6). Hence, by inference they make a Brownian search for a period that will be proportional to the time they might 'expect' their leader to wait for them. Such a Brownian search corresponds to the intensive search phase suggested by Plank and James (Plank and James, 2008) for a seeker that 'knows' that there should be a target in close proximity but in an unknown direction (see also Reynolds, 2009).

We know from our earlier work that the longer tandem runs have proceeded before they were (experimentally) interrupted by the removal of the follower, the longer the leader maintains its stationary wait for its lost pupil (Richardson et al., 2007). Tandem followers often become tandem leaders after a successfully completed tandem run, so it seems reasonable to assume that leaders and followers will be equipped with the same algorithms. Hence, it also seems reasonable to assume that followers should be able to estimate how long their leader would have waited for them at different points along the run. Indeed, the followers who had had their leader removed show significant differences in the rates of their displacement before and after the time at which their leader was likely to have left at IP2 and IP3 (Fig. 6). Differences between the behaviours of both former leaders and former followers at IP1, IP2 and IP3 can be fairly simply explained. Leaders should not wait

long at the first IP because their former follower can easily return to the old nest (85% of former followers returned to the old nest from IP1; Table 2). Indeed, former followers at IP1 make a Brownian search both before and after the lost leader should have left the scene perhaps because they 'know' they are still close to the old nest. By contrast, from IP3, 40% of former followers found the new nest (Table 2). This is both low enough to account for former leaders waiting for longer and sufficiently high to suggest that followers that have been brought so far can sometimes extrapolate successfully beyond the interrupted tandem run to find the new nest (Fig. 5).

We have no evidence that former followers are initially performing a sophisticated search for their former leader. The most sophisticated strategy would be an Archimedean spiral centred on where the target was expected to be. However, executing such a spiral efficiently would require great navigational accuracy (Reynolds, 2008). So a more plausible strategy might involve a looping search. For example, both displaced *Cataglyphis* worker ants searching the location where they 'expect' their nest to be (Wehner and Srinivasan, 1981; Müller and Wehner, 1994; Wehner et al., 2002) or lost honeybee foragers similarly searching for their hive (Reynolds et al., 2007a) [see also Hemptinne et al. (Hemptinne et al., 1996) for a study of apparently spirally searching ladybirds] seem to exhibit looping searches with their paths passing repeatedly through the region where the goal is most likely to be. One fascinating difference for the *T. albipennis* workers looking for a lost leader is that such leaders give up after a while (Richardson et al., 2007) whereas *Cataglyphis* nests or

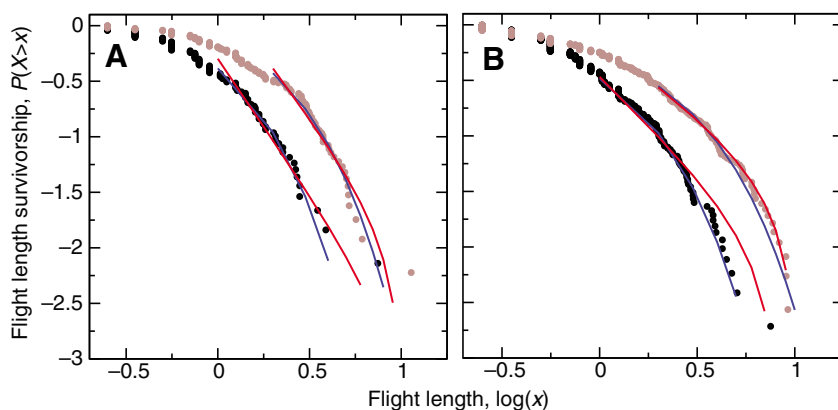


Fig. 9. Flight length frequency distributions of former followers who had their leader removed at different interruption points (IP): (A) IP1, (B) IP2 and IP3 pooled. The panels show the flight length survivorship (the complement of the cumulative distribution function), i.e. the probability *P* of the variable *X* being greater than the value *x* $\{[P(X > x)]\}$ on double-log axes. Flight length distributions at the 'initial' search phase, corresponding to the period before the leader giving-up time' (LGUT) (black dots) and the 'final' search phase, corresponding to the period after the LGUT (brown dots) identified on the basis of individual net-square displacement plots are shown. For visual inspection we also show the exponential (blue) and the truncated power-law (red) fitted 'tail' models in for each distribution.

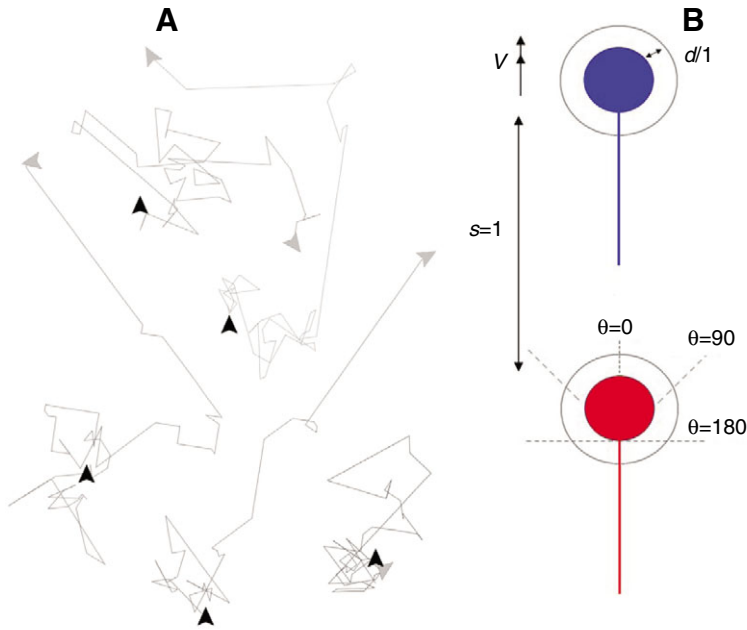


Fig. 10. (A) Five paths of simulated searching followers. The black triangles indicate the starting heading (all 0 deg.) and the grey triangles the end point. (B) Graphical representation of the parameters that were varied in the simulations. The upper 'sunflower' represents the initial position of the leader, and the lower that of the follower. d : pair detection distance, V : leader velocity, θ : possible range of initial follower headings. The initial distance, s , between leader and follower was held constant for all simulations ($s=1$).

beehives do not move. Honeybees searching for ephemeral food sources (Reynolds et al., 2007b), e.g. flowers that might be in the vicinity of those that have bloomed and are no longer producing nectar or pollen, may face a similar problem to lost tandem followers who are searching for a leader that may no longer be present. Here, we have no evidence for an initial looping search but we do appear to see a transition from a Brownian search (which in the short term is likely to be quite local) to a much more wide-ranging search. This transition from an intensive to an extensive search fits the predictions both of Plank and James (Plank and James, 2008) and Reynolds (Reynolds, 2009) for a forager that has found no food after an intensive Brownian search.

Former followers at IP2 and IP3 seem to achieve superdiffusive searches not only by increasing the distances they travel before strong changes of direction but by changing the distribution of these so called flight lengths. Flight lengths are derived from truncated power-law distributions after their former leader should have left the vicinity whereas they are drawn from much less right-skewed distributions during the earlier Brownian search phase when the former leader should still have been nearby (Figs 8 and 9).

At first sight, there may seem to be a contradiction between the Brownian walks and then superdiffusive searches of former tandem followers and the observation that they can extrapolate from the earlier tandem run (Fig. 5). There is no such contradiction because both Brownian and superdiffusive searches can co-exist with 'information-based' drift (Pasternak et al., 2009). Former tandem followers can both 'drift' in the direction they have been shown by the earlier tandem run or in the direction of the 'expected' nearby nest whilst they 'diffuse' first intensively and then extensively by breaking directional correlations on the basis of strong reorientations (Fig. 3) (see also Bartumeus and Levin, 2008). During the search process different former individuals, interrupted at different points, might differ in their use of the drifting and the diffusing search component.

The advantage of a leader waiting stock-still for a lost follower is that they are more likely to reconnect quickly (as shown by our simulation results; Figs 10 and 11). Indeed, not only are the first flights critical but so are the initial body orientations of both parties. The more similar their orientation, the greater is the probability of

them re-establishing contact. Intriguingly, relative body orientation is not only important here between leader and follower but it also matters for the communication between a dancing honeybee and those bees attempting to follow the dance (Judd, 1995). Our simulations also show that if the leader moves off at any appreciable rate the probability of the follower successfully reconnecting is much lower (Figs 10 and 11). Hence, a leader should not wait too long and a follower should not search locally for too long. How long leaders wait, when contact from their follower has been lost, is likely to have evolved through the mutual tuning of the behaviour patterns of both leaders and followers. Once the searching follower's lost leader has left for the new nest, the chance that the pair will be reunited will progressively diminish to become vanishingly small (Fig. 11). This begs the question – for what are such former followers searching when they have adopted a superdiffusive trajectory? Our results show that many former followers find either the old or the new nest and these may approximate sparse and spatially haphazard targets. However, our observation that 12% of leaders deprived of their follower find other ants to lead in the hinterland between the old and new nests, suggests that searching followers might also find new leaders. These are almost certain to be rare and random in their distribution.

If our surmise is correct, that convoluted searches are likely to corrupt an ant's path integrator (Müller and Wehner, 1988), then former followers that eventually stumble upon the new nest will not 'know' how they got there, even though on average they may have drifted in the right direction and gained useful information even from a partial tandem run (Fig. 5). In earlier work, we demonstrated experimentally that active ants that were transferred to the new nest by hand, and were thus lost, often subsequently followed reverse tandem runs (Franks et al., 2009). Such reverse tandem runs serve to bring lost scouts into an active role in emigrations. Pratt has shown for another emigrating *Temnothorax* species that many tandem runs break-up before getting all of the way to the new nest (Pratt, 2008). Thus, the high frequency of reverse tandem runs that is observed in emigrations (Franks et al., 2009) is probably explained by the great abundance of these partly disorientated scouts.

The observation that former followers gain some information from partial tandem runs suggests that tandem runs that break-up

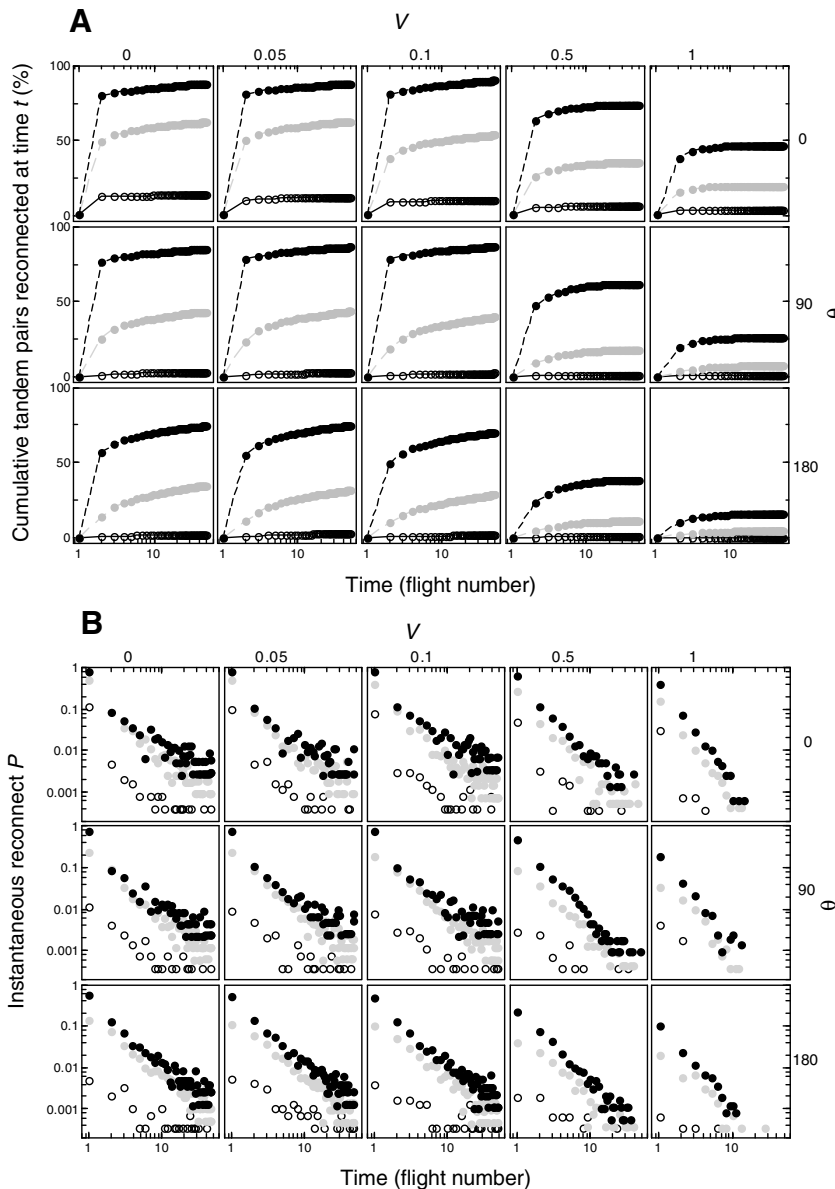


Fig. 11. (A) Simulation results for the success of follower searches over time (1000 simulations for each parameter combination). Follower flights were sampled with replacement from the empirical distributions [for all interruption points (IP) pooled], and follower turn angles between moves were randomly drawn with replacement from a wrapped uniform distribution. See Fig. 10 for explanation of the parameters. Panel columns – leader velocity (V). Panel rows – follower start arc: $\theta=0$ deg., 90 deg., 180 deg. Filled black circle: $d=1.0$, filled grey circle: $d=0.5$, open circle: $d=0.1$. (B) Instantaneous follower reconnection probability as a function of search duration. The instantaneous reconnection probability is calculated as the number of non-cumulative successful reconnections at flight i , divided by the number of followers still searching at flight i . Same data as Fig. 11A.

before arriving at the goal are like anytime algorithms, which return useful, albeit less accurate, results on early termination (Dean and Boddy, 1988; Zilberstein, 1996). Tandem runs increase the probability of followers finding the new nest even if they are interrupted. Tandem runs are literally a move in the right direction and return useful information even if they do not run to completion. In general, we suggest that many sophisticated communication systems in biology will have evolved as anytime algorithms (Dean and Boddy, 1988; Zilberstein, 1996).

Sophisticated structures and behaviour patterns should only evolve if their less sophisticated predecessors enhanced the fitness of the organisms that exhibited them? Thus, for example, the answer to the children’s riddle – ‘which came first, the chicken or the egg?’ is ‘an earlier form of chicken and an earlier form of egg’. It is crucial to evolutionary theory that simpler, less sophisticated and less complete structures or behaviours than those currently exhibited were of adaptive benefit. Thus, Darwin, whilst marvelling at the near perfection of the human eye, needed to suggest plausible simpler stages through which it evolved (Darwin, 1859; Dawkins, 1986). We need to do the same for communication patterns. Our finding

that incomplete tandem runs provide useful information may well suggest that they could have evolved from less sophisticated behaviours. Imagine that at first one ant simply excited another about possible goals by a motor-display in the old nest; later one ant might ‘point’ another nest mate in the right direction through a partial and rudimentary tandem run. Later, remarkably sophisticated and complete tandem runs (Franks and Richardson, 2006; Richardson et al., 2007) might evolve from these simpler yet useful patterns of communication (Hölldobler and Wilson, 1990).

Our results reveal an additional aspect to the precision of the mutual tuning of the behaviour of tandem followers and tandem leaders. Tandem followers moderate their search for their lost leader depending on how far the tandem had proceeded before it broke up. If the follower and leader had travelled sufficiently far, former followers first look for their stationary leader in an intense Brownian search before switching, at almost exactly the time at which their leader would have given up waiting for them, into an extensive superdiffusive search. Evolution thus seems to have tuned the behaviour of teachers (tandem leaders) and pupils (tandem followers) to be responsive to one another’s goals even when their lessons have been interrupted.

APPENDIX

In our study we perform tests dealing with the following models. (1) TPL (Fig. 8): $f(x)=Cx^{-\mu}$ with $x\in[a,b]$ wherein a and b are the minimum and maximum x value, respectively, μ is the scaling exponent and C is the normalisation constant given by $C=(\mu-1)/(a^{1-\mu}-b^{1-\mu})$. (2) Truncated exponential (Fig. 8): $f(x)=Ae^{-\omega x}$ with $x\in[a,b]$ wherein a and b are the minimum and maximum x value, respectively, A is the normalisation constant given by $A=\alpha/(e^{-\omega a}-e^{-\omega b})$ and ω is the rate parameter or inverse scale parameter λ , i.e. $\omega=1/\lambda$. (3) Exponential (Table 4): $f(x)=Ce^{-\alpha x}$ with $x\in[a,\infty]$ wherein a represents the minimum x value, C is the normalisation constant given by $C=\alpha/(e^{-\alpha a})$ and α is the scale parameter, equivalently λ is the inverse scale parameter, i.e. $\alpha=1/\lambda$.

To perform MC replicates, the random values of the variable x from each of the distributions can be obtained by using the following expressions (inversion method). (1) Truncated power law: $x=[b^{1-\mu}-U(b^{1-\mu}-a^{1-\mu})]^{1/(1-\mu)}$. (2) Truncated exponential: $x=-\ln[U(e^{-\omega a}-e^{-\omega b})+e^{-\omega b}]/\omega$. (3) Exponential: $x=-\ln[U]/\alpha$.

In all the equations, U is a uniformly distributed random variable $U\in[0,1]$.

LIST OF ABBREVIATIONS

AIC	Akaike's Information Criterion
CI	confidence interval
IP	interruption point
KS	Kolmogorov-Smirnov
LGUT	leader giving up time
LR	likelihood ratio
MC	Monte Carlo
r.m.s.	root mean square
SPWMC	sequential point-wise model comparison
TPL	truncated power law
wAIC	Akaike weights

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