

## RESEARCH ARTICLE

### Knowledgeable individuals lead collective decisions in ants

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#### SUMMARY

Self-organisation underlies many collective processes in large animal groups, where coordinated patterns and activities emerge at the group level from local interactions among its members. Although the importance of key individuals acting as effective leaders has recently been recognised in certain collective processes, it is widely believed that self-organised decisions are evenly shared among all or a subset of individuals acting as decision-makers, unless there are significant conflicts of interests among group members. Here, we show that certain individuals are disproportionately influential in self-organised decisions in a system where all individuals share the same interests: nest site selection by the ant *Temnothorax albipennis*. Workers that visited a good available nest site prior to emigration (the familiar nest) memorised its location, and later used this memory to navigate efficiently and find that nest faster than through random exploration. Additionally, these workers relied on their private information to expedite individual decisions about the familiar nest. This conferred a bias in favour of familiar nests over novel nests during emigrations. Informed workers were shown to have a significantly greater share in both recruitment and transport to the familiar nest than naïve workers. This suggests that they were the main determinants of the collective preference for familiar nests, and thus contributed greatly to enhance collective performance. Overall, these results indicate that self-organised decisions are not always evenly shared among decision-makers, even in systems where there are no conflicts of interest. Animal groups may instead benefit from well-informed, knowledgeable individuals acting as leaders in decisions.

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Key words: private information, social information, collective decision-making, leader, self-organisation, memory

#### INTRODUCTION

In large animal groups lacking global communication systems, the coordination of collective activities often relies on self-organised mechanisms, i.e. collective patterns emerge from interactions between individuals following simple behavioural rules in response to local information. Self-organisation was thus shown to underlie various natural collective processes in both invertebrates and vertebrates, including humans (Bonabeau et al., 1997; Camazine et al., 2001; Couzin and Krause, 2003; Sumpter, 2006; Moussaid et al., 2009). Self-organised biological processes are fundamentally distributed and do not require any global overview or central control. It has thus long been assumed that group members are interchangeable, following the same set of local behavioural rules and contributing equally to the collective process (Conradt and Roper, 2005; Dyer et al., 2008). This view was particularly widespread in studies on insect societies, where collective complexity and flexibility were often juxtaposed with individual simplicity and homogeneity (Deneubourg and Goss, 1989; Deneubourg, 1995; Bonabeau et al., 1997; Detrain and Deneubourg, 2002; Theraulaz et al., 2003; Detrain and Deneubourg, 2006). However, there is accumulating evidence that certain self-organised processes can be disproportionately influenced by key individuals playing the role of effective leaders. This has been mainly studied

in synchronised movements and activity shifts by large groups of vertebrates (Couzin et al., 2005; Sumpter et al., 2008; Dyer et al., 2009; Lusseau and Conradt, 2009) and invertebrates (Schultz et al., 2008). In insect societies, such as ant and honeybee colonies, recent studies have also highlighted the key influence of specialised and/or experienced individuals on task performance (Robson and Traniello, 1999; Sendova-Franks et al., 2010), division of labour (Anderson and Ratnieks, 1999; Gordon, 2002) and mass recruitment (Collignon and Detrain, 2011). However, most studies of collective decision-making still consider that self-organised, multiple-choice decisions are organised in a 'democratic' way, i.e. evenly shared among decision-makers that follow similar rules (Conradt and Roper, 2005; Seeley, 2010). Although a recent study predicted the existence of leaders in cases where there are significant conflicts of interest among group members (Conradt et al., 2009), the existence of such leaders in natural self-organised decision-making systems has not been documented so far. Here we provide the first experimental evidence of the existence of such influential individuals in a multiple-choice self-organised decision process by an invertebrate group, namely nest site selection by the house-hunting ant *Temnothorax albipennis*.

House-hunting social insects face the major challenge of selecting the best among several candidate new nest sites during emigrations

(ants) or swarming (honeybees). This is achieved through self-organised mechanisms distributed over a subset of active workers, the scouts (Franks et al., 2002; Visscher, 2007). When they have found a suitable site, scouts start recruiting nestmates *via* tandem running (ants) or waggle dancing (honeybees). Recruits may, in turn, initiate recruitment. As recruitment effort increases with nest site quality, this leads to faster population growth at better nest sites. This difference is further amplified through a quorum-sensing rule: final commitment to a new site is indeed triggered when the population in that site reaches a certain value, or quorum threshold (Pratt et al., 2002). Because the quorum is generally reached earlier at better nest sites, this ensures that the best option is chosen in most cases (Seeley and Visscher, 2004; Pratt et al., 2005; Sumpter and Pratt, 2009). Although only scouts contribute to the decision process, there is no evidence that some of them might be more influential than others in the collective decision. Accordingly, previous models of nest site selection by both ants and honeybees have always assumed that all scouts follow similar rules and have a similar weight in the decision process, depending only on the quality of the site they have encountered (Britton et al., 2002; Pratt et al., 2002; Myerscough, 2003; Pratt et al., 2005; Marshall et al., 2006; Passino and Seeley, 2006; Planqué et al., 2006; Pratt and Sumpter, 2006; Planqué et al., 2007; List et al., 2009; Marshall et al., 2009; Sumpter and Pratt, 2009). Here, we show for the first time that specific individuals among the decision-makers in emigrating ants are disproportionately influential in the colony's final choice.

*Temnothorax albipennis* colonies have been shown to gather valuable information about available nest sites prior to emigration, then retrieve and use it in later emigrations, thus influencing the colony's final choice and improving collective performance (Franks et al., 2007; Stroeymeyt et al., 2010; Stroeymeyt et al., 2011). However, previous studies have focused on colony-level behaviour, and the mechanisms underlying collective exploitation of prior information have not been investigated at the individual level so far. Information about suitable sites is initially gathered by the workers that discover and explore the sites. It could then potentially be stored in two, non-exclusive forms: in a common repository of information, such as pheromones (social information) marking the nest itself or leading to it, or in the memories of informed workers and/or individual-specific chemical marking (private information), frequently used by *Temnothorax* ants (Maschwitz et al., 1986; Aron et al., 1988; Danchin et al., 2004; Wagner and Danchin, 2010). In the latter case, informed individuals accessing this information could play a key role during later emigrations. In this study, we individually marked all workers in a colony to investigate the role of specific individuals and the relative importance of private *versus* social information during emigrations, thus showing that workers possessing private information about familiar nests greatly contribute to the collective preference of these over novel nests.

## MATERIALS AND METHODS

Thirty colonies of *Temnothorax albipennis* Curtis 1854 were collected in Dorset, UK, between May 2008 and April 2010 and brought to Bristol, where they were kept in laboratory conditions (Franks et al., 2003).

### General experimental design

Experiments were carried out in arenas consisting of five interconnected Petri dishes with Fluon-coated walls (Fig. 1). Colonies housed in high-quality artificial nests (old nest, ON in Fig. 1) (Franks et al., 2003; Stroeymeyt et al., 2010) were positioned

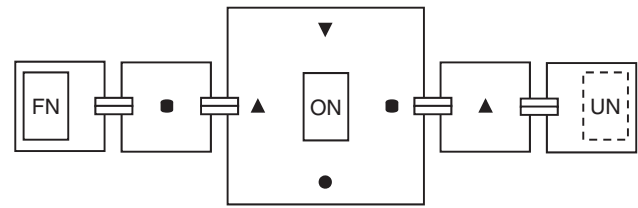


Fig. 1. Top view of the exploration arena consisting of one large central dish, two small intermediate dishes and two small peripheral dishes. Adjacent dishes were connected by tunnels for the ants to walk through. Conspicuous landmarks (black shapes) were used to help ants orientate inside the arena. Colonies housed in their old nest (ON) were positioned in the middle of the central dish. One available nest identical to the old nest was positioned in a peripheral dish at the onset of exploration (familiar nest; FN). Another identical available nest was positioned in the opposite peripheral dish after exploration, at the onset of emigration (unfamiliar nest; UN). The position of new nests (UN and FN) was pseudo-randomised between colonies.

in the middle of the central dish and left to explore the arena for 1 week. Throughout exploration, colonies could freely visit one available nest site, identical to their old nest, positioned at one end of the arena (familiar nest, FN in Fig. 1). We then induced colonies to emigrate by destroying their old nest and simultaneously introduced another identical, never previously encountered nest site at the other end of the arena (unfamiliar nest, UN in Fig. 1). Emigrating colonies therefore had a choice between one familiar and one unfamiliar, otherwise identical, high-quality nest. During emigrations, we recorded emigration-dynamic variables as shown in Fig. 2. Colony distribution was additionally evaluated at the end of emigration by counting the total number of items (brood plus adults) inside each new nest and calculating the proportion of items observed in the familiar nest. A colony was deemed to have chosen a nest only if all brood items were in that nest; otherwise it was considered split.

### Experiment 1: relative roles of informed *versus* naïve individuals

All workers in 10 colonies (median=162.5 workers, range=112–230 workers) were individually marked with unique combinations of coloured paint dots to allow individual identification.

Two webcams (Logitech® QuickCam® Communicate Deluxe, Lausanne, Switzerland) connected to motion detector software Webcam Zone Trigger Version 2.300 Pro (Omega Unfold. Inc., Greenfield Park, QC, Canada) were used to monitor all activity through the entrance of the new nests during emigrations, as explained previously (Stroeymeyt et al., 2010). Both webcams were present during the entire exploration period, and allowed the monitoring of all activity in and out of the familiar nest during exploration.

Picture analysis allowed the identification of all workers that entered the familiar nest during the exploration period, and thereby potentially acquired private information about that nest ('informed' workers). All other workers were considered as 'naïve'. All entrance and exit times were recorded so that we could evaluate the intensity of exploration activity for every informed worker using two measurements: (1) the total number of visits to the familiar nest during exploration and (2) the total time spent inside the familiar nest during emigration. Additionally, for every informed worker we defined the recency of the last visit to the familiar nest as the time elapsed between the end of the last visit and the beginning of

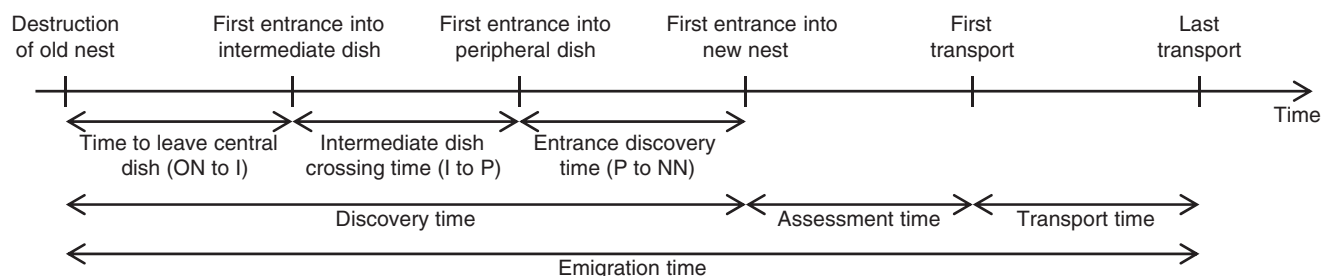


Fig. 2. Colony-level emigration-dynamic variables recorded during the experiments. ON to I, old nest to intermediate dish; I to P, intermediate dish to peripheral dish; P to NN, peripheral dish to new nest.

emigration. Because workers occasionally walked through the nest entrance upside down or lost their paint marks, it was sometimes impossible to assign certain events (entrances and exits) to a given worker. However, the percentage of assigned events was high for all colonies (median=98.4%, range=93.6–100%).

Picture analysis also allowed the recording of all entrances, exits and recruitment acts (i.e. tandem running and transport) for both new nests during emigrations. Activity at the entrance was monitored for each new nest until 50% of the brood items had been carried into the nest. Each worker entering either new nest was identified, and the time and nature of their first entrance (i.e. independent discovery, recruitment by tandem running or transport by a nestmate) were recorded. All workers discovering a nest independently or by following a tandem run to it were considered as potential recruiters. Additionally, all workers actually participating in recruitment to either nest were identified and the time and nature of all recruitment acts (i.e. tandem run or transport) were recorded. This allowed the latency to first tandem run (i.e. time between first discovery of the nest and first tandem run led) and/or the latency to first transport (i.e. time between first discovery of the nest and first item carried to the nest) for every recruiter to be determined. Informed workers that were already inside the familiar nest at the beginning of emigration were not included in the analyses of latencies (see below), as we could not define a first discovery time for these workers.

### Experiment 2: navigational memory *versus* chemical orientation

We performed a second experiment to investigate the relative importance of navigational memory and individual-specific chemical trails in the early discoveries of the familiar nest by informed workers (see below) (Maschwitz et al., 1986; Aron et al., 1988). In this experiment, the floors of all dishes and tunnels were covered with fitted acetate sheets, and pairs of identical proximate landmarks were positioned symmetrically in both branches of the arena. One end of the arena was facing the large, unique window in the experimental room, so that workers could potentially use it as a distant landmark and/or rely on the direction of sunlight as a cue to orient within the arena (Collett et al., 2001; Wehner and Müller, 2006).

Just before the onset of emigration, all acetate sheets and proximate landmarks were lifted from the arena. In the control, they were then replaced exactly as before. In the test, all acetate sheets and identical symmetrical landmarks were rotated 180 deg and (where applicable) swapped between opposite branches of the arena, so that any chemicals previously leading from the old nest to the familiar nest would now lead from the old nest to the opposite end of the arena. This procedure should induce a conflict between potential chemical and visual cues and, therefore, help determine which orientation strategy is dominant in these ants.

Each of 20 colonies was tested under both treatments in a pseudo-random order. After experiencing one treatment, colonies were left to rest in a separate Petri dish for more than 1 week before being tested in the second treatment. Colonies that displayed little exploration activity and colonies that prematurely emigrated to the familiar nest during exploration were excluded from the final analyses, as in a previous study (Stroeymeyt et al., 2010), for a sample size in final analyses of  $N=17$  colonies.

### Statistical analyses

All statistical analyses were performed using Minitab version 15.1 (State College, PA, USA) and R version 2.12.0 (R Foundation for Statistical Computing). Colony- and individual-level variables were analysed using a general linear mixed model (GLMM). For each GLMM analysis (see below), we selected the model fitting our data best by using a stepwise backward procedure. Statistical significance was tested using an analysis of deviance with a Type III sum of squares method. Normality and homoscedasticity of residuals were checked using Kolmogorov–Smirnov and Levene's tests, respectively. If residuals were not normally distributed, we applied either log- or power-transformation to the data, or used a non-parametric test if residuals could not be normalised (see below).

In experiment 1, the following GLMM analyses – all including 'colony' as a random factor – were performed: (1) colony-level variables (discovery time, number of tandem runs, time of tandem runs and time of first transport) were compared among nests using 'nest' (familiar *versus* unfamiliar) as a fixed factor; (2) number of independent discoverers, individual independent discovery times and times of first transport for each transporter were analysed using 'nest', 'information' (informed *versus* naïve) and their interaction as fixed factors; (3) individual latencies to first tandem run were analysed using 'nest', 'information', the covariate 'time of first discovery' and their interactions as fixed factors; (4) individual latencies to first transport were analysed using 'nest', 'information', 'first recruitment act' (tandem run *versus* transport), the covariate 'time of first discovery' and their interactions as fixed factors; and (5) number of items carried per transporter was analysed using 'nest', 'information', 'first recruitment act', 'nature of first entrance' (independent *versus* tandem run *versus* transport) and their interactions as fixed factors.

In experiment 2, the following GLMM analyses – all including 'colony' and 'replicate' as random factors – were performed: (1) emigration time and colony distribution at the end of emigration were analysed using 'treatment' (0 *versus* 180 deg) as a fixed factor; and (2) discovery time and exploration variables [i.e. 'ON to I' (old nest to intermediate dish), 'I to P' (intermediate dish to peripheral dish) and 'P to NN' (peripheral dish to new nest)] were analysed

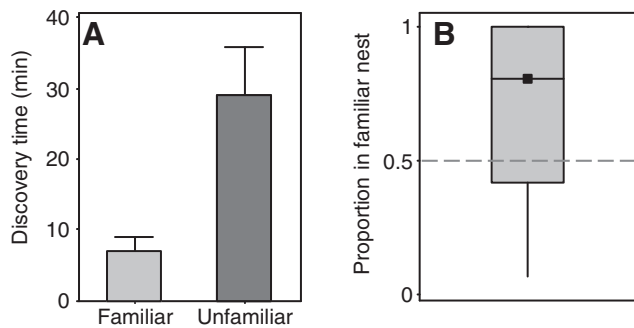


Fig. 3. (A) Discovery time of familiar (light grey;  $N=10$ ) and unfamiliar (dark grey;  $N=10$ ) nests in experiment 1. Data are means  $\pm$  s.e.m. (GLMM, no data transformation,  $F_{1,9}=9.351$ ,  $P<0.05$ ). (B) Proportion of colony (queen, workers and brood) observed in the familiar nest at the end of emigration ( $N=10$ ). Full squares, rectangles and whiskers represent the median, interquartile range and full range, respectively. The broken line represents expectations under the hypothesis of random choice between both nests (one-sample Wilcoxon test with expected median of 0.5,  $P=0.067$ ).

using 'treatment', 'new nest site' (familiar *versus* unfamiliar) and their interaction as fixed factors.

In experiment 1, colony distribution at the end of emigration could not be normalised and was therefore tested using a one-sample Wilcoxon test with a null hypothesis of random choice. Individual propensity to lead tandem runs to either nest among informed and naïve workers was analysed by comparing the number of potential recruiters with the number of actual tandem leaders using Pearson chi-squared and Fisher's exact tests.

## RESULTS

### Experiment 1: relative roles of informed *versus* naïve individuals

Analysis of all exploration visits ( $N=7311$ , median=723.5 per colony, range=46–1149) allowed the identification of 281 informed workers (median=28.5 workers per colony, range=11–42) representing 16.8% (median; range=9.2–25.2%) of the colony's total workforce. Analysis of all emigration visits ( $N=4710$ ; familiar nest, median=301.5 visits per colony, range=82–525; unfamiliar nest, median=128.5, range=12–550) allowed the identification of 875 workers involved in emigrations (familiar nest, median=63 workers per colony, range=21–82; unfamiliar nest, median=24.5, range=3–101). Among these, 353 workers – including 225 informed and 128 naïve workers – actively participated in recruitment and/or transport to either new nest.

#### Colony-level emigration data

During emigrations, familiar nests were discovered significantly earlier than unfamiliar nests (GLMM,  $P<0.05$ ; Fig. 3A). At the end of emigration, colonies appeared to prefer familiar over unfamiliar nests, but this trend was marginally non-significant, probably because of the low sample size used here (five colonies split and five chose the familiar nest; exact binomial test,  $P=0.062$ ; data including split colonies, one-sample Wilcoxon test,  $P=0.067$ ; Fig. 3B).

#### Independent discoveries

During emigrations, naïve workers (i.e. workers which had not previously visited either nest) were as likely independently to find the familiar as the unfamiliar nest (GLMM, Tukey's *post hoc* test,

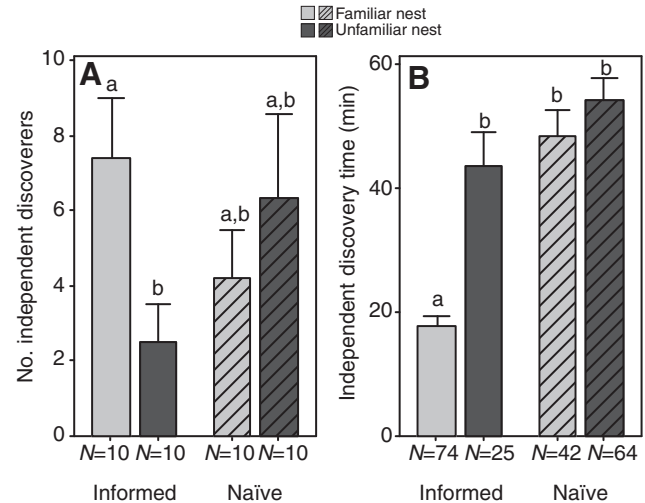


Fig. 4. (A) Number of independent discoverers per colony and (B) time of individual independent discoveries for familiar (light grey) and unfamiliar (dark grey) nests in experiment 1. Data are presented separately for informed (open bars) and naïve workers (hashed bars). Data are means  $\pm$  s.e.m. (GLMM, number of discoverers was log-transformed and discovery time was power-transformed, nest  $\times$  information, no. discoverers,  $F_{1,27}=5.43$ ,  $P<0.05$ ; discovery time,  $F_{1,192}=10.088$ ,  $P<0.005$ ). Different lowercase letters indicate significant differences (Tukey's *post hoc* test,  $P<0.05$ ).

$P=0.97$ ; Fig. 4A) and took a similar amount of time to find either nest (GLMM, Tukey's *post hoc* test,  $P=0.27$ ; Fig. 4B). This suggests that naïve workers did not have any information at their disposal about the location of either nest, but instead randomly searched the arena.

By contrast, informed workers (i.e. workers which had visited the familiar nest prior to emigration) were significantly more likely independently to find the familiar than the unfamiliar nest (GLMM, Tukey's *post hoc* test,  $P=0.038$ ; Fig. 4A). Additionally, those informed workers that went to the familiar nest found it significantly faster than those that went to the unfamiliar nest (GLMM, Tukey's *post hoc* test,  $P<0.0001$ ; Fig. 4B). Informed workers heading to the familiar nest were also significantly faster than naïve workers (GLMM, Tukey's *post hoc* tests, informed/familiar *versus* naïve/familiar,  $P<0.0001$ ; informed/familiar *versus* naïve/unfamiliar,  $P<0.0001$ ; Fig. 4B). The intensity of prior exploration activity by informed workers and the recency of their last visit to the familiar nest did not influence their likelihood of heading towards the familiar rather than the unfamiliar nest (GLMM on the first nest discovered with binomial error structure, effects of total number of visits,  $\chi^2=0.14$ , d.f.=1,  $P=0.71$ ; total visit time,  $\chi^2=0.284$ , d.f.=1,  $P=0.59$ ; recency of last visit,  $\chi^2=0$ , d.f.=1,  $P=1.00$ ). Additionally, there was no effect of these parameters on independent nest discovery times by informed workers (supplementary material Fig. S1). Familiar nests were found by informed workers earlier than unfamiliar nests independently of how much information these workers possessed about the familiar nest.

Overall, our results indicate that informed workers accessed information about the location of the familiar nest, allowing them to find that nest faster than by random exploration. Because naïve workers were apparently unable to use that information, it appears that the information used by informed workers was private at that time.

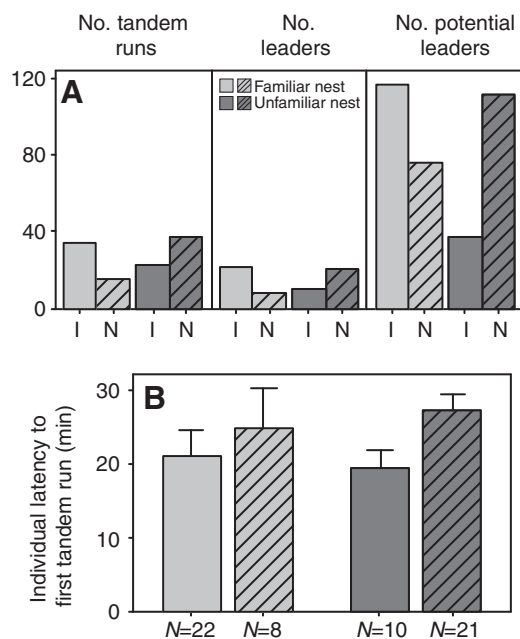


Fig. 5. (A) Number of tandem runs led, number of tandem leaders and number of potential recruiters among informed (I; open bars) and naïve (N; hashed bars) workers at familiar and unfamiliar nests. Data are pooled across colonies. (B) Individual latencies to first tandem run (i.e. time interval between the first entrance into the nest and the first tandem run led) to familiar and unfamiliar nests for informed and naïve tandem leaders. Data are means  $\pm$  s.e.m. (GLMM, no data transformation, nest  $\times$  information,  $F_{1,47}=0.06$ ,  $P=0.81$ ; nest,  $F_{1,47}=0.04$ ,  $P=0.85$ ; information,  $F_{1,47}=1.23$ ,  $P=0.27$ ).

#### Recruitment by tandem running

Overall, similar numbers of tandem runs were led to familiar and unfamiliar nests (GLMM,  $F_{1,9}=0.460$ ,  $P=0.52$ ). However, informed workers had a significantly greater share in tandem running to the familiar than to the unfamiliar nest (Fisher's exact test on tandem runs,  $P<0.005$ ; Fig. 5A). This was not due to differences in the likelihood of informed and naïve workers becoming a tandem leader to either nest (Pearson's chi-squared test on potential recruiters and tandem leaders,  $\chi^2=3.53$ , d.f.=3,  $P=0.32$ ), or to differences in the number of tandem runs individually led by informed and naïve leaders (Pearson's chi-squared test on tandem leaders and tandem runs,  $\chi^2=0.80$ , d.f.=3,  $P=0.85$ ). Investment by informed leaders in tandem running to either nest was also independent of how much they had explored the familiar nest prior to emigration (supplementary material Fig. S2). Rather, the higher contribution of informed workers to recruitment at the familiar nest appeared to be due to the higher proportion of informed workers present and, therefore, available to recruit at the familiar nest (Fisher's exact test on potential recruiters,  $P<0.001$ ; Fig. 5A), which resulted in an overrepresentation of informed workers among tandem leaders at that nest (Fisher's exact test on tandem leaders,  $P<0.001$ ; Fig. 5A).

Additionally, tandem runs to familiar nests occurred earlier than tandem runs to unfamiliar nests during the emigration process. However, this trend disappeared when time of first discovery of the nest was taken into account (familiar nest,  $N=49$ ; unfamiliar nest,  $N=60$ ; GLMM, time since emigration start,  $F_{1,98}=11.037$ ,  $P<0.001$ ; time since first discovery,  $F_{1,98}=1.576$ ,  $P=0.21$ ; supplementary material Fig. S3), and there were no differences in individual

latencies to tandem running across nests (Fig. 5B). Additionally, informed workers did not differ in their latencies to tandem running depending on the intensity of their prior exploration activity or the recency of their last visit to the familiar nest (supplementary material Fig. S2). Hence, the observed differences between nests in the timing of tandem runs can, with reasonable confidence, be attributed to corresponding differences in discovery times.

#### Transport

Informed workers had significantly lower latencies to first transport (i.e. time between first discovery and first transport) to the familiar nest than naïve workers (GLMM, Tukey's *post hoc* tests,  $P<0.0001$ ; Fig. 6A). This, combined with the earlier discoveries of the familiar nest by informed workers, resulted in informed workers initiating transport to that nest earlier in the emigration than naïve workers (GLMM, Tukey's *post hoc* test,  $P<0.0001$ ; supplementary material Fig. S4). As a consequence, informed transporters individually carried significantly more items to the familiar nest than naïve transporters (GLMM, Tukey's *post hoc* test:  $P<0.0001$ ; Fig. 6B).

By contrast, informed and naïve workers had similar latencies to first transport at the unfamiliar nest and initiated transport to that nest at similar times after the onset of emigration (GLMM, Tukey's *post hoc* tests, latency to first transport,  $P=0.99$ ; time of first transport since the beginning of emigration, unfamiliar nest,  $P=0.18$ ; Fig. 6A, supplementary material Fig. S3). As a result, informed and naïve workers had similar individual contributions to transport to the unfamiliar nest (GLMM, Tukey's *post hoc* test,  $P=0.65$ ; Fig. 6B).

Because informed workers individually contributed more to transport to the familiar nest than naïve workers, and because their proportion among transporters was higher at the familiar nest than at the unfamiliar nest (Fisher's exact test,  $P<0.0001$ ; Fig. 6C), informed workers overall had a significantly greater share in transport to the familiar than to the unfamiliar nest (Fisher's exact test,  $P<0.0001$ ; Fig. 6D).

Prior exploration activity did not influence the number of items carried per informed transporter (supplementary material Fig. S5). Interestingly, however, informed workers varied in their latency to first transport depending on their prior exploration activity: workers that made more visits and spent more time overall inside the familiar nest during the pre-emigration period subsequently had significantly lower transport latencies to that nest, whereas no such trend was observed for the unfamiliar nest (GLMM, nest  $\times$  no. visits,  $P<0.001$ ; nest  $\times$  total visit time,  $P<0.05$ ; Fig. 6E). Additionally, workers that had visited the familiar nest a short time before emigration took longer to commit to the unfamiliar nest, whereas no such trend was observed for the unfamiliar nest; however, this trend was marginally non-significant (GLMM, nest  $\times$  recency,  $P<0.063$ ; Fig. 6E). These results suggest a possible role of memory in individual decisions about new nest sites. On the one hand, repeated visits and a long visit time to the familiar nest might act as reinforcers of individual commitment to that nest in the same way as repeated trials with learned information help to consolidate memories. On the other hand, a recent visit to a suitable, familiar nest might interfere with individual commitment to a novel, unfamiliar nest.

Overall, our results therefore indicate that informed workers contributed disproportionately to transport to the familiar nest because they were more likely to participate in transport to that nest, discovered it earlier and took much less time to commit and initiate transport to it presumably because they had previously gathered a lot of information about that nest. Because the colony's final choice depends directly on the intensity of transport to each of the candidate

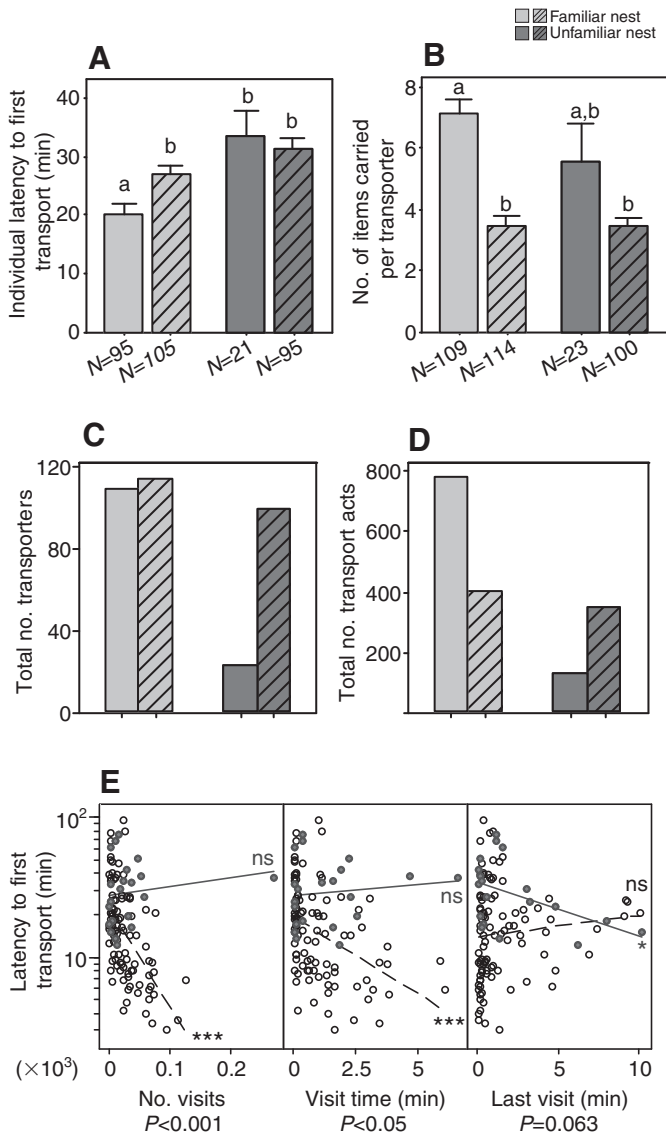


Fig. 6. (A) Individual latencies to first transport (i.e. time interval between the first entrance into the nest and the first item carried) to familiar (light grey) and unfamiliar (dark grey) nests for informed (I, open bars) and naive (N, hashed bars) transporters. Data are means  $\pm$  s.e.m. (GLMM, log-transformation, nest,  $F_{1,300}=6.37$ ,  $P<0.05$ ; information,  $F_{1,300}=20.89$ ,  $P<0.0001$ ; time of first discovery,  $F_{1,300}=40.13$ ,  $P<0.0001$ ; first recruitment act,  $F_{1,300}=10.07$ ,  $P<0.005$ ; nest  $\times$  information,  $F_{1,300}=7.00$ ,  $P<0.01$ ; information  $\times$  time of first discovery,  $F_{1,300}=8.90$ ,  $P<0.005$ ). (B) Number of items carried per transporter during the monitored period. Data are means  $\pm$  s.e.m. (GLMM, log-transformation, nest,  $F_{1,328}=3.44$ ,  $P=0.065$ ; information,  $F_{1,328}=14.53$ ,  $P<0.0001$ ; nature of first entrance,  $F_{1,328}=14.28$ ,  $P<0.0001$ ; first recruitment act,  $F_{1,328}=14.05$ ,  $P<0.0001$ ; nest  $\times$  information,  $F_{1,328}=3.99$ ,  $P<0.05$ ). Different lowercase letters in A and B indicate significant differences (Tukey's *post hoc* test,  $P<0.05$ ). (C) Total number of informed and naive transporters at familiar and unfamiliar nests in experiment 1 (Fisher's exact test,  $P<0.0001$ ). Data are pooled across colonies. (D) Total number of transport acts by informed and naive workers at familiar and unfamiliar nests in experiment 1 (Fisher's exact test,  $P<0.0001$ ). Data are pooled across colonies. (E) Latency to first transport to familiar (open circles, hashed lines) and unfamiliar (filled circles, solid lines) nests for informed transporters as a function of: (1) the total number of visits to the familiar nest during exploration; (2) the total time spent in the familiar nest during exploration; and (3) the recency of the last visit to the familiar nest. Each point represents one informed worker (GLMM, log-transformation, nest  $\times$  number of visits,  $F_{1,115}=12.49$ ,  $P<0.001$ ; nest  $\times$  total visit time,  $F_{1,114}=6.19$ ,  $P<0.05$ ; nest  $\times$  recency of last visit,  $F_{1,113}=3.54$ ,  $P=0.063$ ). The relationships were best described by the following equations: (1) familiar nest,  $\log(\text{latency})=1.37-0.00011(\text{visit time})$  ( $r^2=0.18$ ,  $F_{1,93}=19.50$ ,  $P<0.001$ ); unfamiliar nest, non-significant (ns) regression ( $r^2=0.02$ ,  $F_{1,20}=0.49$ ,  $P=0.49$ ); (2) familiar nest,  $\log(\text{latency})=1.29-0.0072(\text{no. visits})$  ( $r^2=0.33$ ,  $F_{1,94}=44.28$ ,  $P<0.001$ ); unfamiliar nest, non-significant regression ( $r^2=0.01$ ,  $F_{1,20}=0.28$ ,  $P=0.60$ ); (3) familiar nest, non-significant regression ( $r^2=0.01$ ,  $F_{1,94}=0.91$ ,  $P=0.34$ ); unfamiliar nest,  $\log(\text{latency})=1.54-0.000038(\text{last visit time})$  ( $r^2=0.23$ ,  $F_{1,20}=5.76$ ,  $P<0.05$ ).

greatly affect search, even in the control (GLMM, effect of nest,  $F_{1,46}=3.482$ ,  $P=0.07$ ; nest  $\times$  treatment,  $F_{1,45}=0.263$ ,  $P=0.61$ ).

Despite their initial hesitation in the central dish, test colonies did not differ from control colonies in the crossing times of intermediate dishes and in the time to find the entrance for either nest (GLMM, effect of treatment,  $F_{1,44}\leq 1.451$ ,  $P>0.23$ ; nest  $\times$  treatment,  $F_{1,44}\leq 1.727$ ,  $P>0.19$  for both variables). In both treatments, intermediate dishes leading to the familiar nest were crossed faster than those leading to the unfamiliar nest, and the entrance was found faster for familiar than for unfamiliar nests (GLMM, effect of nest, I to P,  $F_{1,45}=14.071$ ,  $P<0.001$ ; P to NN,  $F_{1,44}=16.546$ ,  $P<0.001$ ; Fig. 7B). This resulted in familiar nests being discovered significantly earlier than unfamiliar nests in both treatments (GLMM, effect of treatment,  $F_{1,47}=3.704$ ,  $P=0.06$ ; effect of nest,  $F_{1,47}=18.726$ ,  $P<0.001$ ; treatment  $\times$  nest,  $F_{1,46}=1.284$ ,  $P=0.26$ ; Fig. 7B). Overall, these results suggest that chemical cues, if any, had little influence on the orientation process, and that ants instead mostly relied on visual cues memorised during the individual explorations prior to emigration.

## DISCUSSION

Our results show that individuals that had visited the familiar nest prior to emigration (informed workers) possessed personal knowledge about its location. They were indeed more likely to head towards the familiar nest and were able to find it significantly faster than an equidistant unfamiliar, novel nest. By contrast, workers that had not previously visited the familiar nest (naïve workers) were unable to use that information and instead randomly explored the arena. Because it remained inaccessible to naïve

nest sites, our results imply that informed workers strongly influenced the collective decision.

## Experiment 2: navigational memory *versus* chemical orientation

Colonies emigrated significantly faster when potential chemical cues were not rotated (control) than when they were rotated 180 deg (test; Fig. 7A). However, colony distribution at the end of emigration was similar for both treatments, with a significant preference for the familiar nest (one-sample Wilcoxon test on pooled data,  $N=34$ ,  $P<0.001$ ; Fig. 7A). This indicates that test colonies had been able to exploit prior information about the familiar nest in spite of the rotation of chemical cues. The longer emigration time observed in the test was probably due to an initial period of hesitation: test colonies were indeed slower to leave the central dish than control colonies, suggesting that they were initially disturbed by the experimental procedure (GLMM, ON to I, effect of treatment,  $F_{1,46}=5.141$ ,  $P<0.05$ ; Fig. 7B). However, in both treatments, workers heading towards the familiar nest and workers heading towards the unfamiliar nest left the central dish at similar times, indicating that, at this early stage, prior information about the familiar nest did not

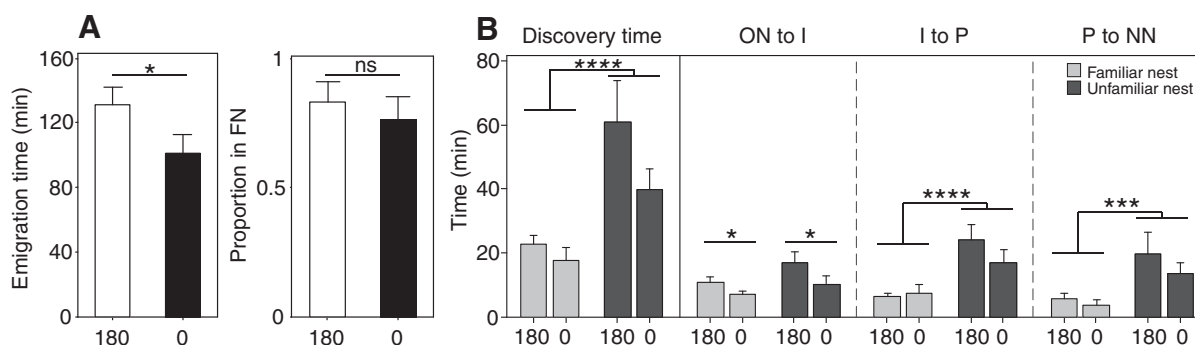


Fig. 7. (A) Emigration time and proportion of the colony in the familiar nest (FN) for test (white bars; 180 deg rotation) and control (black bars; 0 deg rotation) colonies in experiment 2 [GLMM, no data transformation, effect of treatment, emigration time,  $F_{1,14}=5.801$ ,  $P<0.05$ ; proportion in FN,  $F_{1,14}=0.539$ ,  $P=0.48$ ]. (B) Discovery time, time to leave the central dish (ON to I), crossing time of the intermediate dish (I to P), and nest entrance localisation time (P to NN) of the familiar and unfamiliar nest for test and control colonies (GLMM, log-transformation of all variables). Data are means  $\pm$  s.e.m.; \*\*\*\* $P<0.001$ ; \*\*\* $P<0.005$ ; \* $P<0.05$ ; ns, not significant.

nestmates, the personal knowledge of informed workers therefore constituted private information (Danchin et al., 2004; Wagner and Danchin, 2010). Informed workers could rely on at least two types of private information: navigational memories allowing them to find the familiar nest using visual cues in the environment, and individual-specific chemical trails leading from the old nest to the familiar nest. Although both strategies are well documented in *T. albipennis* and related *Temnothorax* species [navigational memory (Aron et al., 1988; Pratt et al., 2001; McLeman et al., 2002); individual-specific trails (Maschwitz et al., 1986; Aron et al., 1988)], our results suggest that memory of visual cues strongly dominates over chemical orientation in the present context. The 180 deg rotation of all chemicals did not impair the ability of workers to discover the familiar nest earlier than the unfamiliar nest during emigrations and did not modify the colonies' overall preference for the familiar nest. The rotation of chemical cues did induce transient confusion within the central dish, possibly due to the disturbance of the familiarity markers used, as previously shown in *Temnothorax* sp. (Aron et al., 1986). However, this manipulation did not affect the scouts' ability to orient to and find the familiar nest quickly after this initial hesitation period. This suggests that when these two sources of information are conflicting, navigational memories based on visual cues strongly dominate over chemical orientation, as observed previously in other ant species [e.g. *Temnothorax unifasciatus* (Aron et al., 1988) and *Lasius niger* (Aron et al., 1993; Grüter et al., 2011)]. In this scenario, explorer ants acquired private information about the predictive relationships between the familiar nest and distant landmarks and/or menotactical cues (i.e. light direction), and thereafter predominantly relied on these visual cues when navigating between the old nest and the familiar nest. Whether ants used a prominent landmark as a beacon to guide their paths to the nest or a constellation of landmarks whose relative position allowed locating the nest in a map-like manner (Collett and Graham, 2004) remains to be determined.

In addition to information about its location, informed workers also appeared to have information about the suitability of the familiar nest. Informed workers indeed showed significantly lower latencies from first discovery to first transport at the familiar nest than at the unfamiliar nest, i.e. they took less time to commit fully to the familiar nest. This could be partly due to the quorum threshold being reached earlier in the familiar than in the unfamiliar nest, because: (1) there were usually already a few informed workers (median=3,

range=0–7) inside the familiar nest at the onset of emigration and (2) the initial increase in the population should be faster for the familiar nest, because both independent discoveries by informed workers and tandem running occur earlier. However, there was no evidence that naïve workers could exploit such information, as they appeared just as slow to initiate transport to both nests. This shows that information about the suitability of familiar nests was at least partly private. Informed workers varied in their speed of commitment to the familiar nest depending on the intensity of their prior exploration activity, and in their speed of commitment to the unfamiliar nest depending on the recency of their last visit to the familiar nest. These results suggest a possible role of memory in individual decisions by informed workers about new nest sites. Further investigations will help confirm or refute that hypothesis.

Overall, the use of private information by informed workers resulted in: (1) overrepresentation of informed workers, (2) earlier independent discoveries and (3) faster individual commitment to the familiar nest. This had a strong impact on the collective decision-making process by inducing an earlier start of the subsequent steps of emigration (tandem running and transport) for the familiar nest, which in turn resulted in familiar nests being preferred over unfamiliar nests in the final choice of colonies. Although this trend was marginally non-significant (binomial test,  $P=0.062$ ), this was probably due to the low sample size used here ( $N=10$ ), imposed by the need to mark all of the workers individually. Indeed, if the choice pattern remained the same, adding only two colonies to our sample would have resulted in a significant  $P$ -value in the binomial test (six colonies choosing the familiar nest and six colonies splitting would result in  $P=0.032$ ). Additionally, a highly significant preference for the familiar nest was previously observed in a study using exactly the same experimental design with a higher sample size [proportion of colony in the familiar nest, median=0.81,  $N=10$ ,  $P=0.067$  (present study); median=0.83,  $N=33$ ,  $P<0.001$  (Stroeymeyt et al., 2010)]. The high similarity of the medians (0.81 versus 0.83) strongly suggests that the overall preference of the colonies was similar in both studies, and that the difference in statistical significance was mainly due to the difference in sample sizes (10 versus 33). Therefore, the preference for the familiar nest observed here can be considered biologically meaningful with reasonable confidence.

Informed workers played a highly influential role in the colony's final decision by following different behavioural rules from those of naïve workers. Indeed, whereas naïve workers behaved similarly towards both nests, the prior experience of informed workers with

the familiar nest modified and biased their behaviour towards that nest during the search phase (non-random exploration) and during the assessment phase (faster commitment). This contrasts with previous assumptions about house-hunting ants and the honeybee, where all individuals were assumed to follow the same rules depending only on the quality of the sites encountered during emigrations (Britton et al., 2002; Pratt et al., 2002; Myerscough, 2003; Pratt et al., 2005; Marshall et al., 2006; Passino and Seeley, 2006; Planqué et al., 2006; Pratt and Sumpter, 2006; Planqué et al., 2007; List et al., 2009; Marshall et al., 2009; Sumpter and Pratt, 2009). The behavioural diversity observed here presumably conferred more weight to knowledgeable workers in the decision process. Indeed, collective choices in house-hunting ants strongly depend both on tandem running to reach a consensus, and on transport to implement the decision. Our results clearly show that informed workers had a greater share in both tandem running and transport to the familiar nest than naïve workers, because they were more numerous there and their individual contributions to transport to that nest were higher. Informed workers, which had previously memorised valuable information, were therefore the main determinants of the colony's preference for the familiar nest. Previous results indicate that this preference is highly beneficial for the colony, as it leads to increased collective performance in terms of speed, accuracy and group cohesion (Stroeymeyt et al., 2010). Knowledgeable workers thus play a key role in allowing the collective exploitation of valuable private information.

Key individuals were already predicted to play a major role in certain self-organising processes, such as synchronised movements in large groups (Couzin et al., 2005; Schultz et al., 2008; Sumpter et al., 2008; Conradt et al., 2009; Dyer et al., 2009) and division of labour in social insect colonies (Robson and Traniello, 1999). Our study highlights a new instance of a self-organised biological process in which all individuals do not contribute equally to the collective outcome, i.e. multiple-choice collective decision-making in an invertebrate. This contrasts with the common belief that self-organised decisions should be democratically shared among decision-makers, unless there are conflicts of interests among group members (Conradt et al., 2009). We show that knowledgeable individuals may also have a disproportionate influence and lead collective decisions when group members share the same interests. Although self-organised systems appear very effective under the assumption that all individuals follow the same simple set of rules (Bonabeau et al., 1997; Camazine et al., 2001), the presence of key, well-informed individuals altering their behaviour according to their prior experience might generally enhance performance even further, e.g. by allowing the fine-tuning of collective processes. We predict this to be of general importance in collective decision-making with no conflicts of interests: diverse mechanisms may enable the entire group to benefit from the private knowledge, experience and/or aptitudes or skills of specific individuals. Therefore, we expect future research to identify new, previously overlooked cases of collective decisions involving disproportionately influential individuals.

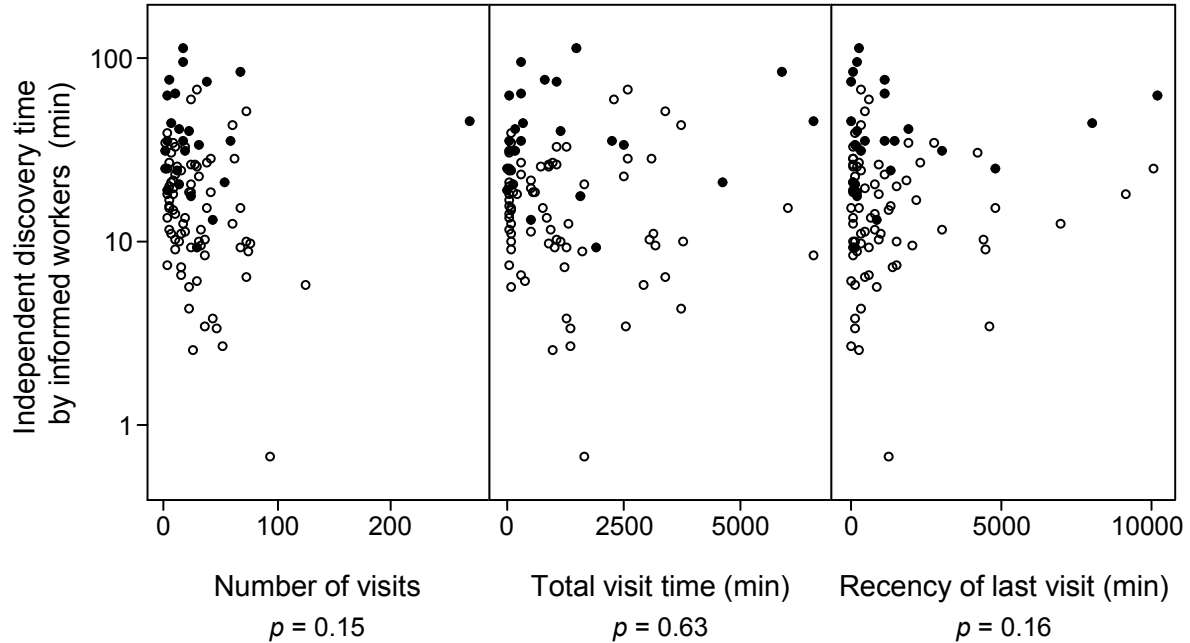
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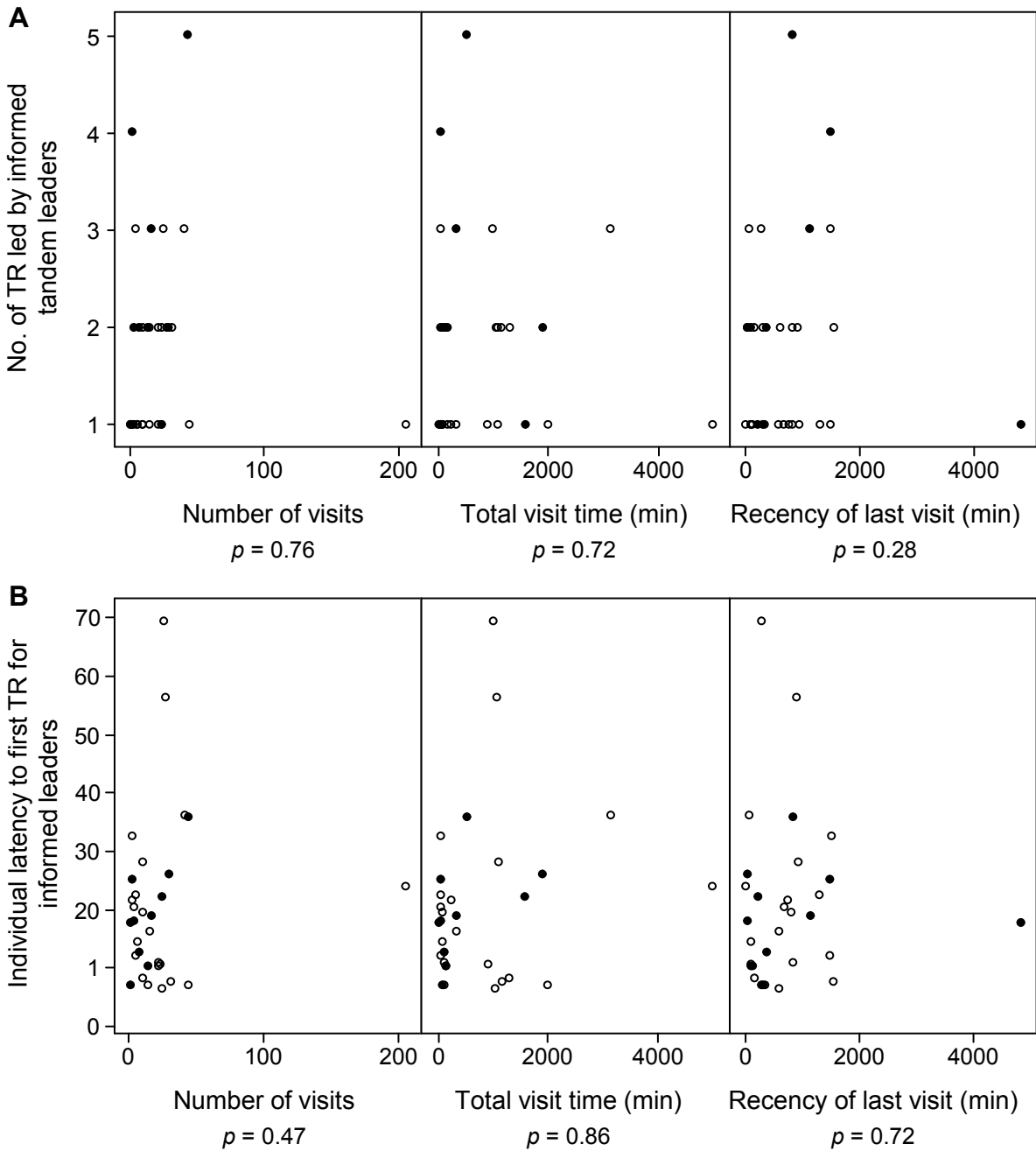
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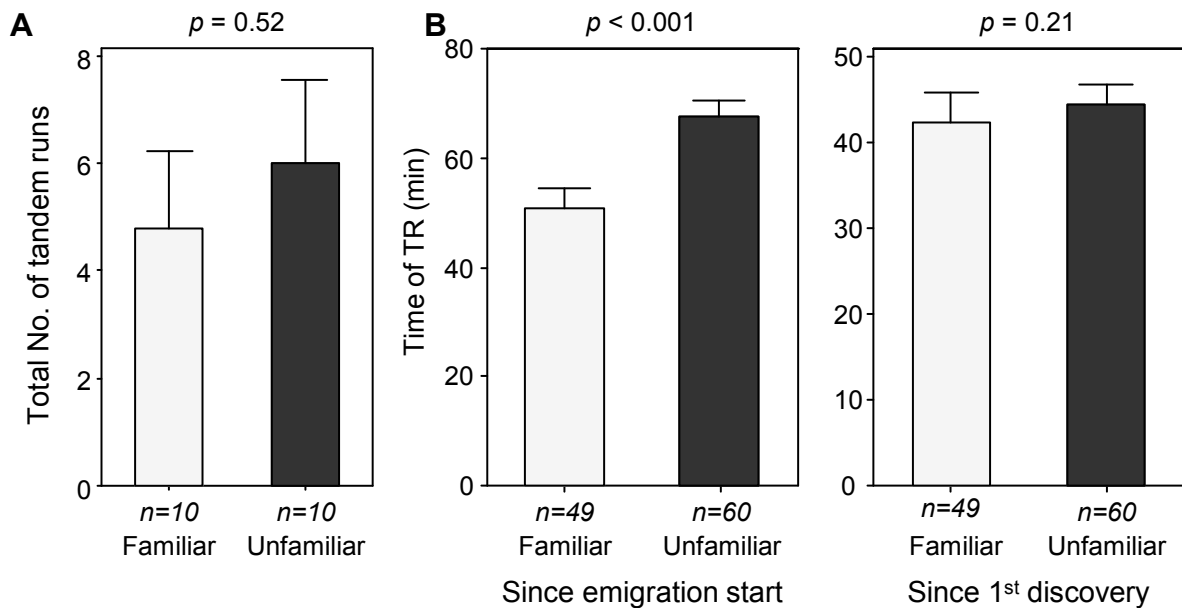
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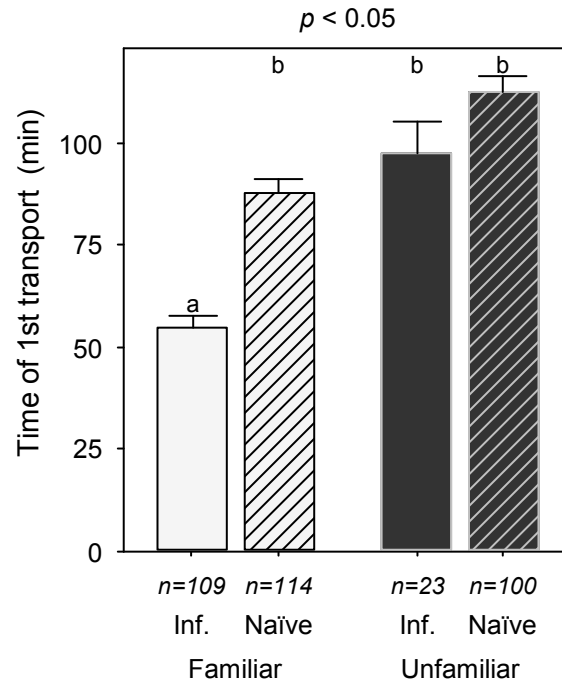
**Fig. S1.** Time of independent discoveries of familiar (open circles) and unfamiliar (full circles) nests by informed workers as a function of (i) the total number of visits of the familiar nest during exploration; (ii) the total time spent in the familiar nest during exploration; and (iii) the recency of the last visit to the familiar nest. Each point represents one informed worker (GLMM; discovery times were log-transformed; effects of ‘Number of visits’:  $F_{1,87} = 2.147$ ,  $p = 0.15$ ; ‘Total visit time’:  $F_{1,86} = 0.230$ ,  $p = 0.63$ ; ‘Recency of last visit’:  $F_{1,87} = 2.034$ ,  $p = 0.16$ ; ‘Nest’:  $F_{1,88} = 19.268$ ,  $p < 0.001$ ; interaction with ‘Nest’:  $F_{1,85/86} < 1.1$ ,  $p > 0.3$  for all three variables).



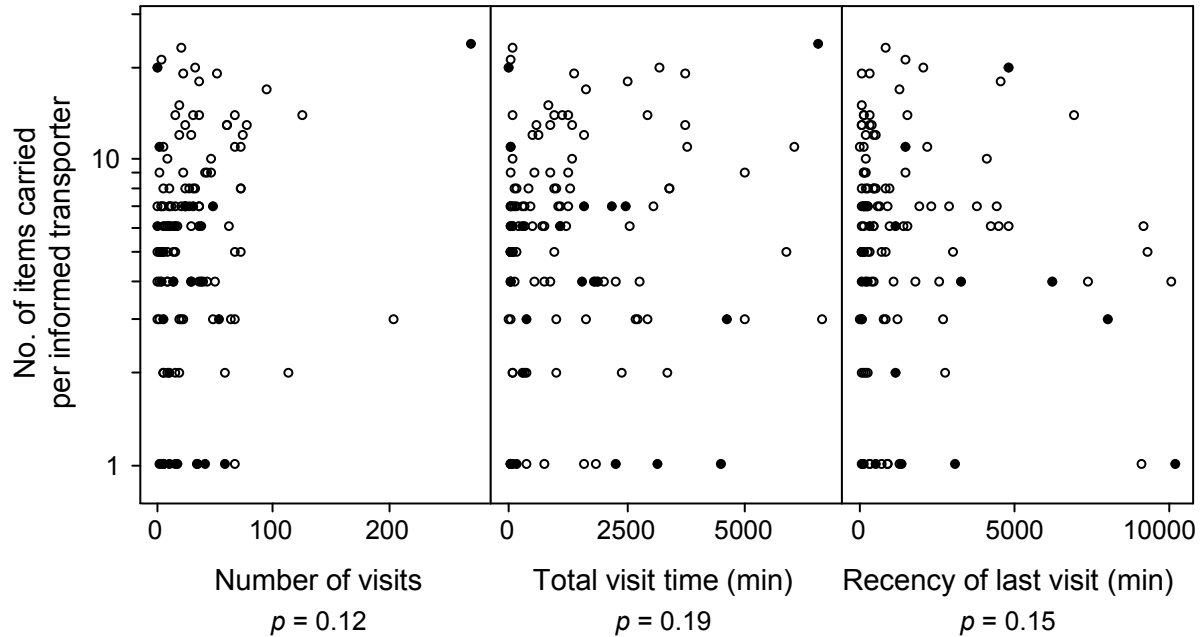
**Fig. S2.** (A) Number of tandem runs (TR) led and (B) individual latency to first tandem run to familiar (open circles) and unfamiliar (full circles) nests by *informed* tandem leaders as a function of (i) the total number of visits of the familiar nest during exploration; (ii) the total time spent in the familiar nest during exploration; and (iii) the recency of the last visit to the familiar nest. Each point represents one informed worker (GLMM; No. of TR was power-transformed; *No. of tandem runs*: effects of ‘Number of visits’:  $F_{1,30} = 0.10$ ,  $p = 0.76$ ; ‘Total visit time’:  $F_{1,30} = 0.13$ ,  $p = 0.72$ ; ‘Recency of last visit’:  $F_{1,30} = 1.25$ ,  $p = 0.28$ ; ‘Nest’:  $F_{1,30} = 0.18$ ,  $p = 0.67$ ; interaction with ‘Nest’:  $F_{1,30} < 1.6$ ,  $p > 0.2$  for all three variables; *Latency to first tandem run*: effects of ‘Number of visits’:  $F_{1,30} = 0.54$ ,  $p = 0.47$ ; ‘Total visit time’:  $F_{1,30} = 0.86$ ,  $p = 0.37$ ; ‘Recency of last visit’:  $F_{1,30} = 0.13$ ,  $p = 0.72$ ; ‘Nest’:  $F_{1,30} = 0.17$ ,  $p = 0.68$ ; interaction with ‘Nest’:  $F_{1,30} < 1.92$ ,  $p > 0.18$  for all three variables).



**Fig. S3.** (A) Total number of successful forward tandem runs to familiar (light grey) and unfamiliar (dark grey) nests in experiment 1. (B) Tandem run times to familiar and unfamiliar nests since the start of emigration or since the first discovery of the nest. Bars and whiskers represent means and standard errors, respectively (GLMM; no data transformation; effect of ‘Nest’; no. of tandem runs:  $F_{1,9} = 0.460$ ,  $p = 0.52$ ; time since emigration start:  $F_{1,98} = 11.037$ ,  $p < 0.001$ ; time since first discovery:  $F_{1,98} = 1.576$ ,  $p = 0.21$ ).



**Fig. S4.** Time of first transport to familiar and unfamiliar nests for informed and naïve transporters since the start of emigration. Bars and whiskers represent means and standard errors, respectively (GLMM; no data transformation; effect of ‘Nest’:  $F_{1,333} = 11.39$ ,  $p < 0.001$ ; ‘Information’:  $F_{1,333} = 32.73$ ,  $p < 0.0001$ ; interaction ‘Nest’  $\times$  ‘Information’:  $F_{1,333} = 5.16$ ,  $p < 0.05$ ). Same letters indicate no differences, whereas different letters indicate significant differences ( $p < 0.05$ ) in Tukey’s post-hoc tests.



**Fig. S5.** Number of items carried per *informed* transporter to familiar (open circles) and unfamiliar (full circles) nests as a function of (i) the total number of visits of the familiar nest during exploration; (ii) the total time spent in the familiar nest during exploration; and (iii) the recency of the last visit to the familiar nest. Each point represents one informed worker (GLMM; power-transformation; effects of ‘Number of visits’:  $F_{1,131} = 2.4$ ,  $p = 0.12$ ; ‘Total visit time’:  $F_{1,130} = 1.74$ ,  $p = 0.19$ ; ‘Recency of last visit’:  $F_{1,118} = 2.06$ ,  $p = 0.15$ ; ‘Nest’:  $F_{1,131} = 0.62$ ,  $p = 0.43$ ; interaction with ‘Nest’:  $F_{1,118-131} < 1.89$   $p > 0.17$  for all three variables).