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Better the nest site you know: decision-making during nest migrations by the Pharaoh's ant

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Abstract Animals frequently have to decide between alternative resources and in social insects these individual choices produce a colony-level decision. The choice of nest site is a particularly critical decision for a social insect colony to make, but the decision making process has still only been studied in a few species. In this study, we investigated nest selection by the Pharaoh's ant, *Monomorium pharaonis*, a species renowned for its propensity to migrate and its use of multi-component trail pheromones to organise decision-making in other contexts. When presented with the choice of familiar and novel nests of equal quality in a Y set-up, colonies preferentially migrated towards the familiar nest, suggesting a form of colony-level 'memory' of potential nest sites. However, if the novel nest was superior to the familiar nest, then colonies began migrating initially to the familiar nest, but then redirected their migration to the superior quality novel nest. This may be an effective method of reducing colony exposure while searching for an optimum nest site. Branches that had previously led to a selected nest were attractive to ants in subsequent migrations, suggesting that trail pheromones mediate the decision making process. The adaptive, pheromone-based organisation of nest-site selection by Pharaoh's ants matches their ephemeral environment and is likely to contribute to their success as a 'tramp' species.

Keywords Latent learning · Social insect · Pheromone · Nest site selection · Trail

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Introduction

Animals are often required to make decisions between alternative resources. Whether foraging, selecting mates, avoiding predation or choosing nest sites, the resulting decision determines their subsequent fitness (Krebs and Kacelnik 1993; Blumstein and Bouskila 1996). While many decisions are between two novel resources, others may be between focusing on an existing resource or searching for a new, better quality resource. Group-living animals such as social insects face the same decisions, but these are also influenced by interactions between group members. Groups may reach combined decisions, in which individuals choose relatively independently, or consensus decisions, in which individuals choose with the aim of reaching a consensus in order to maintain group cohesion and retain the benefits of group-living (Conradt and Roper 2005). The latter are characteristic of eusocial species, such as the social insects. These exhibit self-organisation in which individuals respond to local stimuli according to simple rules and thereby produce a group-level response, rather than the group being directed by a leader (Bonabeau et al. 1997; Boomsma and Franks 2006). Information on the alternatives is transferred from informed to uninformed individuals to recruit the latter towards a resource. The resulting positive feedback is frequently non-linear, with the proportion of individuals making a particular choice increasing sharply when a quorum threshold is reached (Sumpter and Pratt 2009).

Effective decision-making is particularly critical for social insect colonies during nest site selection. Migrating between nest sites is energetically costly and carries high risks in many species, while selecting a suboptimal nest site will reduce colony fitness; therefore a trade-off arises (Bartholomew et al. 1988; Healey and Pratt 2008). However, nest migration behaviour has only been well studied in a few species (reviewed by Visscher 2007). Generally, scout individuals locate alternative nest sites and recruit nestmates by waggle dancing (in honey bees), tandem running, and direct transport of nestmates or trail pheromones (in ants).

One of the best-studied examples of nest site selection is the rock ant *Temnothorax albipennis*. These ants nest within cavities and discriminate between nests following a weighted additive strategy, preferring those that are darker, of an appropriate area for their colony size, and have narrower or fewer entrances (Mallon et al. 2001; Franks et al. 2003b, 2005, 2006). Individual scouts assess potential nest sites and then recruit nestmates through tandem running until a quorum threshold of individuals in the new nest is reached, at which point the ants change to transporting nestmates, which is several times faster (Pratt et al. 2002). Individual ants need not make direct comparisons of alternatives; instead, they initiate recruitment at a higher rate to high-quality nest sites and are less likely to switch to searching for alternatives, resulting in positive feedback that produces a colony-level decision (Mallon et al. 2001; Robinson et al. 2009). Ants become more committed to the choice as the migration progresses and transport at a lower quorum threshold when conditions are harsh (Franks et al. 2003a; Planqué et al. 2007). If presented with a choice between a more proximate poor-quality nest and a more distant superior nest, ants may initially migrate to both simultaneously, but all traffic switches to the superior nest midway through the migration (Franks et al. 2008). Intriguingly, the colony-level decision making process appears to include a form of colony-level 'memory'. Colonies presented with a choice between familiar and novel poor quality nests, select the novel nest (Franks et al. 2007), and colonies familiar with high quality nests both prefer and are able to emigrate faster to these sites than colonies naive to them (Stroeymeyt et al. 2010), suggesting colony-level 'memory' of nest sites to avoid as well as ones to actively seek. *Temnothorax* ants orientate using both visual landmarks and trails of pheromone marks (McLeman et al. 2002), and the colony-level 'memory' has been suggested to be due to both landmark memory by individual ants and repellent pheromones (Franks et al. 2007; Stroeymeyt et al. 2011a).

Unlike *T. albipennis*, Pharaoh's ants (*Monomorium pharaonis*) do not use visual landmarks, and instead rely solely on the chemistry and geometry of their trails for directional cues (Sumpter and Beekman 2003; Jackson et al. 2004). They are also the only ant known to use a repellent pheromone to organise their trails, which they do in the context of foraging (Robinson et al. 2005). Pharaoh's ants use a positive feedback, mass recruitment system when foraging, involving the independent trail laying and following behaviour of worker ants (Sudd 1960; Sumpter and Beekman 2003). Trails can vary in both pheromone components and concentrations in order to convey different information to uninformed individuals (Jackson and Châline 2007; Jackson et al. 2007). Pharaoh's ants use a long-lived attractive pheromone to mark territory and allow reestablishment of foraging trails, a short-lived attractive pheromone to mark a trail to a resource, and a short-lived repellent pheromone to mark non-rewarding branches of trail bifurcations (Jeanson et al. 2003; Robinson et al. 2005, 2008; Jackson et al. 2006). The use of three pheromones provides both a record of past resources, and allows for the exploitation of ephemeral resources in a changing environment via the short lived and repellent pheromones. Here we investigate the nest migration behaviour of Pharaoh's ants. This species is a highly successful 'tramp' species, in large part because colonies migrate very readily and frequently split to reproduce by budding (Hölldobler and Wilson 1990). This is likely an adaptation to the ephemeral nature of many of the cavities in which they nest opportunistically and suggests that emergency migrations are probably common. We first investigate the nest attributes preferred by Pharaoh's ants during a nest migration, and then examine the effect of familiarity on decision making.

Methods

We studied four colonies of Pharaoh's ants which each contained 200–400 workers, 10–15 queens and brood of various stages. Colonies were maintained in plastic boxes (53×33×17 cm) at 25±3°C, 85±5% RH, 12:12 L/D cycle, on a diet of *Tenebrio* larvae, honey water, and ant diet (Keller et al. 1989). Colonies were provided with an artificial nest, consisting of a plastic box (79×47×5 mm), with a 4-mm-wide entrance hole, and a glass lid raised on matchsticks (2 mm wide) placed along the border of the box (Fig. 1). Nest migrations were initiated by removing the lid of nests. Experiments were conducted at the same time of day to avoid circadian variation in ant activity affecting the results. Any nest apparatus that was reused after an experiment was cleaned with warm water and detergent in order to remove any pheromone, and left for at least 24 h as a further precaution to allow the evaporation of any pheromone traces (Jackson et al. 2006).

Experiment 1: nest preferences

In order to determine the nest characteristics preferred by the ants, colonies were provided with test nests that differed in one of three variables: (1) height — tall (79×47×6 mm) or short (79×47×3 mm); (2) area — large (73×73×3 mm) or small (79×47×3 mm); (3) light — light (cover of red acetate [LEE filter 019FIRE], some light entering around the edge) or dark (cover of metal foil, with minimal light entering around the edge). The test nests in each case were otherwise

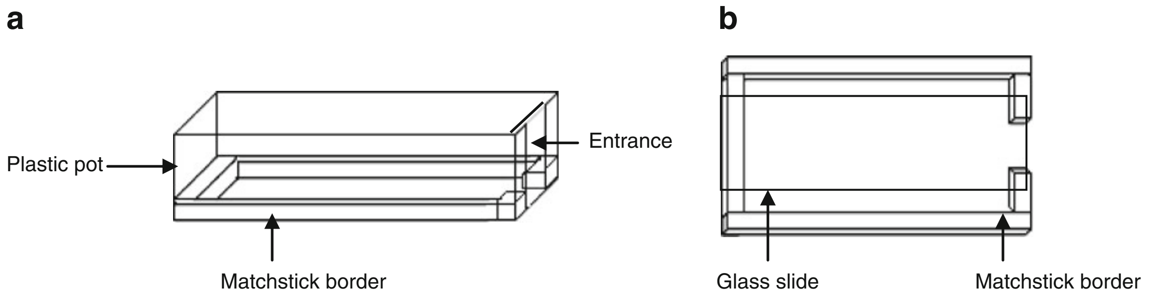

Fig. 1 The most attractive nest type in Experiment 1. This nest consisted of a plastic pot (79×47×5 mm) with a small central entrance (4 mm wide) (**a**). Inside was a border of matchsticks (height 3 mm, width 2 mm) (**b**). A glass slide (76×26 mm) was placed on top of the matchstick border to form the top of the nest; for the tall nests, a second layer of matchsticks were carefully positioned on top of the first

identical to the standard nest design, which was short, small and light. To assess each variable, two test nests (tall and short, large and small or light and dark) were placed in the foraging arenas at equal distances from the inhabited nest (55 cm from start nest, 33 cm apart). The entrances of the test nests were both positioned to face the inhabited nest entrance. Migrations were initiated and the numbers of ants within the original nest and each of the two test nests were estimated by counting at 10-min intervals for 60 min. The time at which the brood was moved was also recorded, as well as the final colony nest choice after 3 h. For the light experiment, the foil cover prevented the number of ants within the dark nest being directly counted, so they were instead calculated by deducting the sum of the numbers of ants in the light nest, original nest, and elsewhere in the arena, from the total number of ants in the colony. For each of the three variables, we carried out four (area and light experiments) or five (height experiment) migrations for each of the four colonies (52 migrations in total). Following each migration, colonies were forced to migrate back into a standard (short, small, light) nest and left for at least 12 h.

Experiment 2: the effect of familiarity

Based on Experiment 1 (see results), three nest types were designed: a high-quality nest (tall, small, dark), a medium-quality nest (tall, small, light) and a poor-quality nest (short, big, light). To test preference for two alternative nest types, a Y-shaped acetate bridge was made by attaching two branches (10×1.5 cm) to a main stem (12.5×1.5 cm) with split pins (cotter pins) with a 60° angle between the branches. The two test nests were placed at the end of each branch, 8 cm above the floor (on raised platforms) with the stem of the Y-shape sloping to the floor where the original nest was located. Fluon coatings (Whitman Plastics Ltd.) ensured ants could only access the test nests via the upper surface of the Y-shaped bridge. A new Y-shaped bridge was used for each replicate. Colonies started each experimental trial in medium quality nests. One branch (alternately left or right) leading to a poor-quality nest was attached to the stem of the Y-shaped bridge. The ants were left to become familiarised with this alternative nest for 3 days, during which many ants were observed to visit it. The other branch was placed in the foraging arena, far from the food and water resources, for the 3-day familiarisation period. By exposing the control branch to the ants in this way, we aimed to avoid possible effects of novel area exploration, or positive pheromones laid to food or water resources. The use of a poorer quality nest than that inhabited avoided unprompted migrations, while the absence of the second branch on the Y-shaped bridge during the familiarisation period prevented it being marked by negative pheromones (Robinson et al. 2005). After the familiarisation period, the second branch was added to the Y-shaped bridge, and led to a novel, poor-quality nest that was identical to the familiar nest. Migrations were then immediately initiated. To assess the immediate migration process, the numbers of ants passing a point 1 cm from the Y-bifurcation along each branch during 30 s, and the branch choice of every individual arriving at the junction for 2 min were recorded every 3 min for 15 min. The time at which the brood was moved as well as the final nest choice by the colony after 3 h was also recorded. Five migrations were carried out for each of the four colonies (20 migrations in total).

Experiments 3a and 3b: traffic concentration and nest familiarity

We carried out two experiments to examine whether previously raised branches may be intrinsically attractive due to a concentration of ant traffic during the familiarization process, or if it is the combination of both this branch traffic and nest familiarity that guides migrating colonies. First, in Experiment 3a, we provided each colony with only the Y-shaped bridge in the same set up as used in Experiment 2, with one attached (raised) branch (but with no nest at the end of the raised branch) and one detached branch flat on the arena floor. Following the 3-day familiarisation period, migrations were initiated to nests of equal quality placed at the end of branches that had either been raised or laid flat on the floor. Second, in Experiment 3b, we provided each colony with the same set up as in Experiment 2, except that the control branch was left connected to the Y-shaped bridge and led to an empty platform rather than being laid flat on the arena floor. After the familiarisation period, a novel nest was placed on the empty platform and migrations immediately initiated. As before, we recorded the branch traffic and individual choices over a period of 15 min, the time at which the brood was moved, and final nest choice after 3 h. Five migrations were carried out for each of the four colonies per experiment (20 migrations in total for each experiment).

Experiment 4: nest familiarity vs. nest quality

The same procedure was followed as in Experiment 2, except that while the familiar nest was of poor quality, the novel nest was of superior quality. In addition, recordings of ant numbers in this experiment were continued for 30 min to allow for the possibility of migrations changing direction, the time at which the brood was moved, and again final nest choice after 3 h recorded. Five migrations were carried out for three of the colonies, and four migrations for one of the colonies (19 migrations in total).

Experiment 5: the role of pheromones in nest choice

Following each replicate in Experiments 2 and 4, we conducted an immediate follow-up experiment to test whether pheromone trails were guiding nest migrations. To do this, the nest chosen by (and therefore containing) the colony was moved to the location of the original nest, the Y-shaped bridge apparatus removed and the colony left for 1 h. If the colony had split between two nests during the first migration, the nest containing the most ants was used, with ants from the other nest being added to it to reunite the colony. Each colony was then provided with a medium quality nest at the end of each branch of the Y-shaped bridge and migrations immediately initiated. One of the branches (alternately left or right; random with respect to previous position) was a branch that had led to a nest selected by the same colony in either Experiment 2 or 4, and was therefore potentially marked with positive recruitment pheromone. The other (control) branch had been placed in the foraging arena, far from the food and water resources, for the 3-day familiarisation period as described in Experiment 2, and was therefore presumed to be unmarked with any recruitment pheromones. As before, branch traffic and individual choices were recorded. Four migrations were carried out for each colony using branches from Experiment 2, and four (two colonies) or five (the other two colonies) migrations were carried out using branches from Experiment 4 (34 migrations in total).

Statistical analysis

We analysed all data in R 2.11.1 (R Development Core Team 2010) using linear mixed-effect models fitted by maximum likelihood, implemented using the lmer function in the lme4 package (Bates and Maechler 2010), except in the case of Experiment 4 where we used a generalized additive mixed model implemented using the gamm4 function (Wood 2011). We analysed the data in two ways. First, we analysed the number of ants in each nest at the final observation point of the experiment (for Experiment 1) or both the total traffic counts and the individual choices at the final observation (for Experiments 2–5). Here, we fitted a model with number of ants as the response variable, nest type or branch type as the explanatory variable, and colony as a random effect. Second, to explore the change in the number of ants travelling on each branch over the time course of each experiment, we fitted a model with number of ants as the response variable modelled as a function of time with nest or branch fitted as a treatment and with trial nested within colony fitted as the random term. This approach allowed us to assess the interaction over time between the two nests or branches, which indicated whether or not a preference for one or the other nest or branch developed over the course of the migration. Finally, to confirm that the counting methods correlated well with the final nest choice after 3 h, we modelled whether the predicted nest choice after 3 h was correct or not as a function of the method used to assess this choice (i.e., number of ants inside nest, traffic on branch, or number of ants choosing branch at the final time point of the experiment), using a binomial error structure. In each analysis we used the likelihood ratio test to generate *P* values and models were checked visually for normality of the residuals and homogeneity of variances (Faraway 2006).

Results

Migration characteristics

Splitting between nests was relatively rare. From the 111 migrations where final nest choice after 3 h was recorded, on only ten occasions did colonies split between nests. The measures of preference we used (number of ants inside the nest, the traffic on the branch and the number of ants choosing a branch at the final time point of the experiment) were reliable predictors of final nest choice after 3 h. Each variable was highly correlated with whether that nest was finally chosen (proportions close to 1), rejected (proportions close to 0) or if the colony split between two nest sites (proportions close to 0.5), indicating that the methods we used were reliable measures of a colonies nest choice (number of ants inside nest: χ^2=5058, *df*=2, P<0.001; traffic on branch: χ^2=681, *df*=2, P<0.001; ants choosing branch: χ^2=1363, *df*=2, P<0.001).On average, the brood began to be moved at 7.9±0.67 (mean±SE) min, showing that migrations were initiated relatively quickly.

Experiment 1: nest preferences

The average number of ants in the starting nest decreased over time, and increased in each of the new nests, demonstrating the migration of the ants (Fig. 2). There were significantly more ants in the dark nest compared to the light nest at 60 min (χ^2=21.48, *df*=1, P< 0.001), and there was a significant interaction between time and nest type showing an increasing preference for the dark nest over the course of the migration (χ^2=101.84, *df*=2, P< 0.001). Although slightly more ants were counted in tall rather than short, and small rather than large nests, in neither case was the preference significant at the final time point (short vs. tall: χ^2=0.939, *df*=1, P=0.332; large vs. small: χ^2=2.29, *df*=1, P=0.129). However, there was a significant interaction seen over the time course of the experiment for the large nest vs. the small nest (χ^2=13.32, *df*=2, P=0.0013), indicating the ants increasing preference for the small nest, but a non-significant difference in preference between the short nest and the tall nest (χ^2= 5.68, *df*=2, P=0.0583).

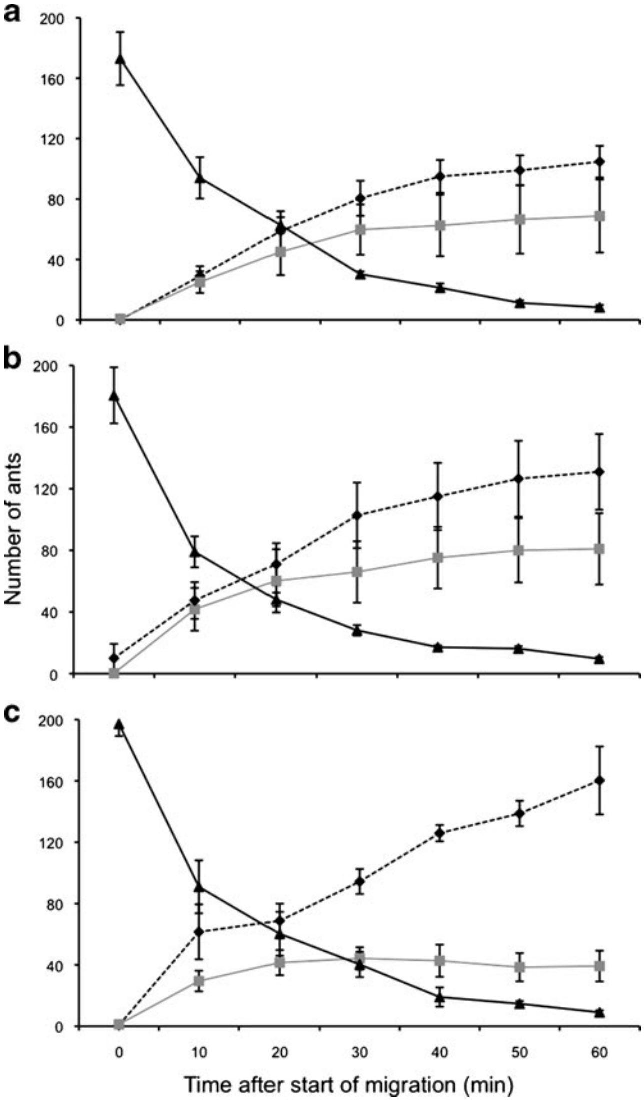

Fig. 2 Selection of different nest attributes in Experiment 1. Mean± SE numbers of ants in either the original nest (*solid black line* and *triangles*) or the two alternative nests provided that were either: **a** short vs. tall, **b** large vs. small or **c** light vs. dark alternative nests (*grey lines and squares* or *dashed lines and diamonds*, respectively, in each)

Experiment 2: the effect of familiarity

The average number of ants increased over time to a greater extent on the familiar branch than on the novel branch (Fig. 3), and the individual branch choice of ants at the Y-bifurcation followed the same pattern. Both branch traffic and branch choice differed significantly between the two branches both at the final timepoint in

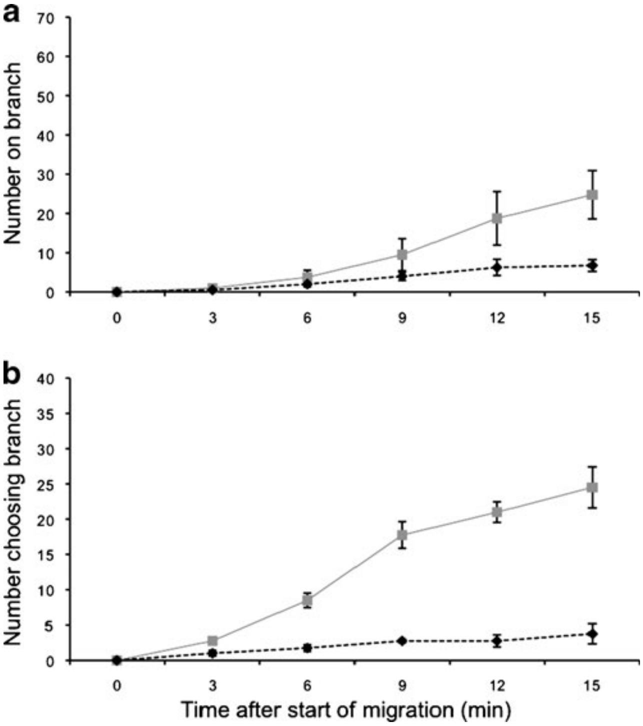

Fig. 3 Selection of familiar vs. novel equal quality nests in Experiment 2. Mean±SE number of ants either travelling along in 2 min (ant traffic; **a**) or choosing in 30 s (branch choice; **b**) branches leading to either familiar (*grey line and squares*) or novel (*dashed line and diamonds*) alternative nests, both of which were of poor quality

the experiment (traffic: $\chi^2=10.47$, $df=1$, $P=0.0012$; individual choices: $\chi^2=15.55$, $df=1$, $P<0.001$), and throughout the course of the experiment (traffic: $\chi^2=52.98$, $df=2$, $P<0.001$; individual choices: $\chi^2=107.96$, $df=2$, $P<0.001$) indicating that ants were choosing the familiar over the novel nest.

Experiment 3a and 3b: traffic concentration and nest familiarity

The average numbers of ants travelling along both the branches that had been raised and those that had been on the floor increased over time, but to a greater extent on the former (Experiment 3a; Fig. 4). At the end point of the experiment there was a non-significant difference in branch traffic ($\chi^2=3.33$, $df=1$, $P=0.068$) but a significant difference in individual choice ($\chi^2=4.32$, $df=1$, $P=0.038$), while over the whole time course of the experiment there was a significant difference between branches in both measures (traffic: $\chi^2=16.40$, $df=2$, $P<0.001$; individual choices: $\chi^2=22.90$, $df=2$, $P<0.001$). This indicated a weak intrinsic attraction towards these raised branches and also no negative labelling of them. In Experiment 3b, we saw a similar but stronger effect when both branches had been raised but one led to a familiar nest, i.e., the average numbers of ants travelling towards the familiar nest increased over time to a much greater extent than the number of ants travelling towards the novel nest (Experiment 3b; Fig. 4). At the end point of this experiment there was a highly significant difference in both branch traffic ($\chi^2=13.55$, $df=1$, $P<0.001$) and individual choice ($\chi^2=11.34$, $df=1$, $P<0.001$), and also over the whole time course of the experiment there was again a highly significant difference between branches in both measures (traffic: $\chi^2=64.52$, $df=2$, $P<0.001$; individual choices: $\chi^2=41.89$, $df=2$, $P<0.001$). Overall these two experiments show that both branch traffic and nest familiarity are important to the migrating ants.

Experiment 4: nest familiarity vs. nest quality

The average numbers of ants travelling along both the familiar and novel branches increased initially, but to a greater extent on the familiar branches (Fig. 5). Analysis of the numbers of ants on each branch at the midpoint of the experiment showed a significant difference in both branch traffic ($\chi^2=8.47$, $df=1$, $P=0.0036$) and individual ant choices ($\chi^2=14.67$, $df=1$, $P<0.001$) Subsequently, however, the numbers choosing and travelling along the familiar

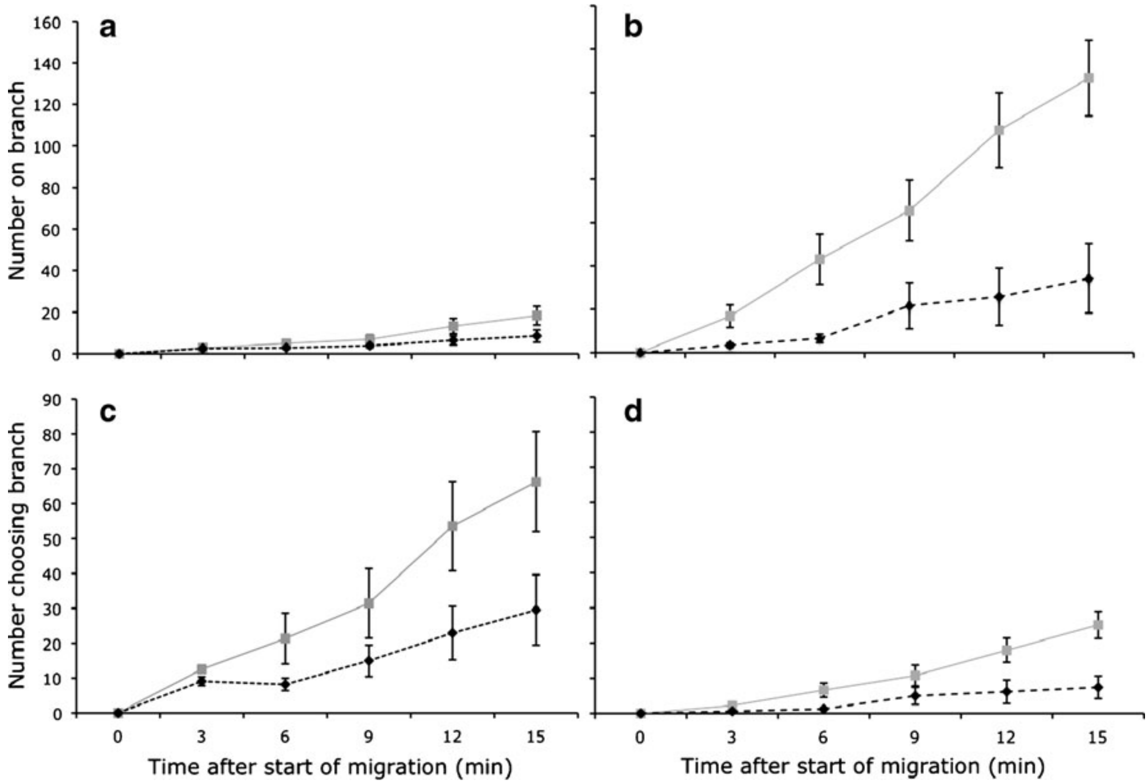

Fig. 4 Selection of branches in Experiments 3a and 3b. Mean±SE number of ants either travelling along in 2 min (ant traffic; **a** and **b** or **b**) or choosing in 30 s (branch choice; **c** and **d**) branches that were either raised for 3 days (*grey lines and squares*) or flat for 3 days (*dashed lines and diamonds*) (Experiment 3a; **a** and **c**) or branches that were raised for 3 days leading to a nest (*grey lines and squares*) or an empty platform (*dashed lines and diamonds*) (Experiment 3b; **b** and **d**)

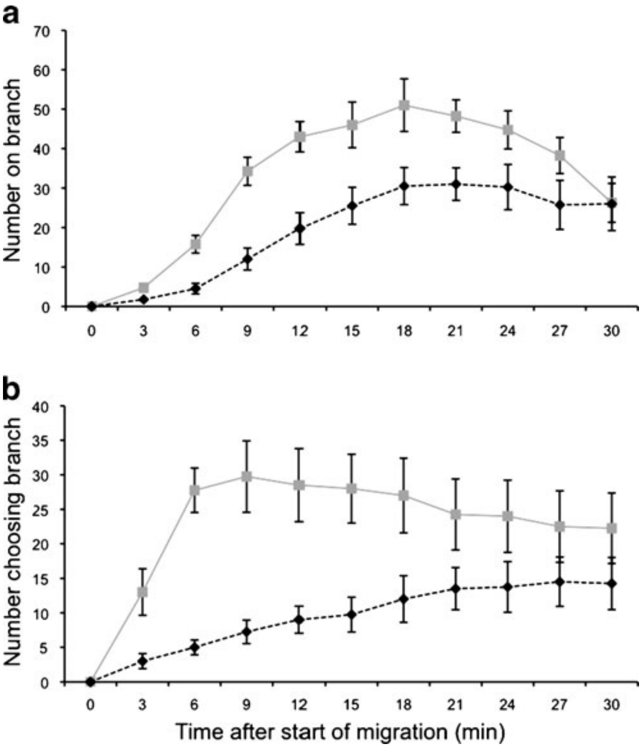

Fig. 5 Selection of familiar vs. novel nests of different quality in Experiment 3. Mean±SE number of ants either travelling along in 2 min (ant traffic; **a**) or choosing in 30 s (branch choice; **b**) the branches leading to either familiar poor quality (*grey line and squares*) or novel superior quality (*dashed line and diamonds*) alternative nests

branch decreased while those on the novel branch remained approximately the same. Consequently, the numbers travelling along the familiar and novel branches were more similar at the end of the 30 min observation period (Fig. 5; traffic: χ^2=0.0402, *df*=1, *P*=0.841; individual choices: χ^2=3.42, *df*=1, *P*=0.0643). Analysis of the entire time course of the experiment showed a significant interaction between branch choice and time (traffic: χ^2=20, *df*=2, $P<0.001$; individual choices: χ^2=21.86, *df*=2, $P<0.001$).

Experiment 5: the role of pheromones in nest choice

The average numbers of ants travelling along both the previously chosen and control branches increased over time. The increase was greater along the previously chosen branches, both for those previously chosen in Experiments 2 and 4 (Fig. 6). When testing branches chosen in Experiment 2, this preference was not significant for branch traffic or individual choice at the end point of the experiment (traffic: χ^2=3.375, *df*=1, *P*=0.123; individual choices: χ^2=2.53, *df*=1, *P*=0.112), but the interaction between branches over time was highly significant (traffic: χ^2=22.72, *df*=2, $P<0.001$; individual choices: χ^2=21.72, *df*=2, $P<0.001$). When testing branches chosen in Experiment 4, the preference was significant for individual choice, but not significant for branch traffic at the end point of the experiment (traffic: χ^2=3.304, *df*=2, *P*=0.0691; individual choices: χ^2=7.91, *df*=1, *P*=0.0049), and both measures were significant over the entire time course of the experiment (traffic: χ^2=35.08, *df*=2, $P<0.001$; individual choices: χ^2=55.57, *df*=2, $P<0.001$).

Discussion

This study investigated decision-making during nest migrations by Pharaoh's ants, *M. pharaonis*. When ants were forced to migrate after destruction of their nest, they tended to migrate towards familiar, rather than novel, nests when they were of equal nest quality. However, when the novel nest was of superior quality, ants tended to switch their choice and change the direction of their migration towards this rather than a lower-quality familiar nest. Our data also suggest that ants are using pheromones to guide migrations towards new nests. The ephemeral lifestyle of Pharaoh's ants means such emergency migrations are likely to be a common challenge for their colonies. It is important to note that Pharaoh's ant colonies may have a critical minimum colony size of around 600 ants in order to form a functioning attractive pheromone trail (Sumpter and Beekman 2003). Our colony sizes of 200–400 ants were considerably smaller than this, so it is very likely that the effects demonstrated here would be much greater with larger colony sizes.

When presented with nest sites differing in light, height, or size, the ants preferred darker nests, and the data suggest that tall and small nests may have been slightly preferred over short and large nests. The ants did not appear to simply apply a satisficing strategy, i.e., opting for the first adequate nest (Franks et al. 2003b), because all nest types were occupied on at least some occasions and were therefore adequate. Instead the ants appear to be actively selecting higher quality nest types. Darkness is apparently important in nest choice, more so than area or height, and a stronger effect still would most likely have been seen if the light nests were fully exposed rather than having a red acetate lid. Darker nests should provide better protection from predators and the environment as they characterise a more enclosed and hence better protected cavity, whereas nest space may only be important in terms of providing sufficient room for brood rearing and avoiding overly large nests that may be hard to protect. Nest area and height are both important characteristics in the nest site selection of *Temnothorax* ants and honey bees, but, at least in the former, are less highly ranked in the weighted additive strategy (Seeley and Buhrman 1999; Mallon and Franks 2000; Mallon et al. 2001; Franks et al. 2003b). The same may be true of Pharaoh's ants.

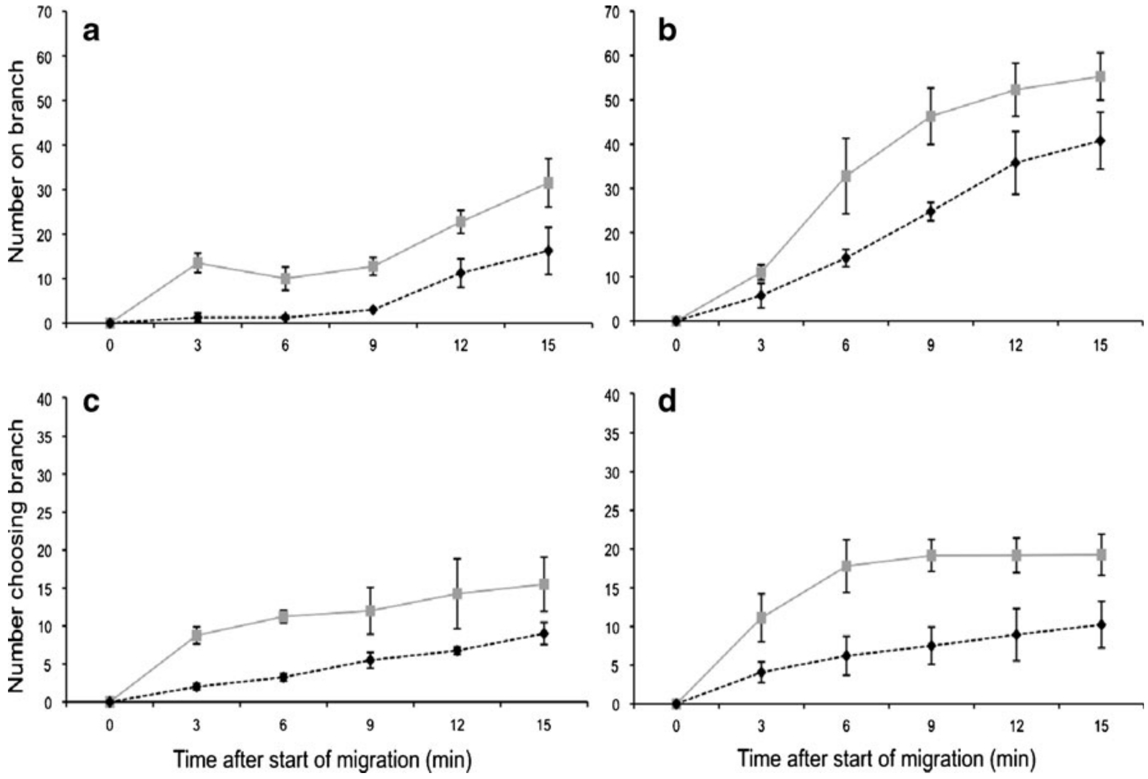

Fig. 6 Use of pheromones in nest choice in Experiment 4. Mean±SE of number of ants either travelling along in 2 min (ant traffic; **a** and **b**) or choosing in 30 s (branch choice; **c** and **d**) either branches previously chosen in Experiment 2 (**a** and **c**) or Experiment 3 (**b** and **d**) (*grey lines and squares*), or a control branch (*dashed lines and diamonds*)

When presented with familiar and novel nests of the same (poor) quality, the ants showed a clear preference, with an increasing number of ants on, and choosing, the branches leading to the familiar nest over the course of the migration. Experiment 3a showed a small but significant preference for nests that were accessed via the ‘previously raised’ branch rather than the ‘previously flat’ branch, indicating a weak intrinsic attractiveness for ‘raised’ branches, most probably due to the concentrating of traffic on them during the familiarisation period. Experiment 3b, however, showed that it is not only the effect of the branch being raised and hence a concentration of traffic that is attractive to the migrating ants, but that there is an effect of nest familiarity over and above that of traffic concentration. Pharaoh’s ants therefore seem to have a form of colony-level ‘memory’ of potential nest sites, making these more attractive in some way. This memory may be similar to that found in *Temnothorax* ants which appear to negatively label and avoid poor quality familiar nests (Franks et al. 2007), and both prefer and can migrate faster than naive colonies to high quality familiar nests (Stroeymeyt et al. 2010, 2011a). Possibly, the poor quality nests we offered to the Pharaoh’s ants may not have been sufficiently poor to warrant negative labelling. Alternatively, it may be that any nest site is attractive to Pharaoh’s ants as a potential refuge should an emergency migration be required, but this remains to be investigated.

It is likely that pheromones play an important part in the colony level preference for familiar nests and the branches leading to them. Pharaoh’s ants are known to use both long-lived and short-lived attractive pheromones during foraging (Sudd 1960; Jeanson et al. 2003; Jackson and Châline 2007; Jackson et al. 2007), and similar mechanisms could be used in nest site selection. Both Experiment 4, and Experiments 3a and 3b, suggested that attractive pheromones are laid to selected nest sites. The short-lived pheromone is too volatile to have still been present on the branches used in Experiment 4 (Jeanson et al. 2003; Robinson et al. 2008), and so it is likely to be the long-lived pheromone, which can persist for up to 48 h (Jackson et al. 2006), that is guiding the ants. About a fifth of foraging Pharaoh’s ant workers are ‘pathfinder scouts’, which are the only individuals capable of detecting the long-lived pheromone (Jackson et al. 2006). These individuals may utilize these long-lived pheromone trails in order to relocate potential nest sites, and during an emergency migration the pathfinders could then activate trails for other workers by applying the short-lived attractive pheromone. It is likely that the long-lived pheromone is laid passively during exploration, and it is the interaction of this with actively laid positive trail pheromone that initiates recruitment (Traniello 1989; Yamaoka and Akino 1994; Devigne and Detrain 2002; Jackson et al. 2004, 2006, 2007; Jackson and Ratnieks 2006). This idea is substantiated by the effect of traffic concentration in Experiment 3a and the effect over and above this of nest familiarity in Experiment 3b.

The ability to retain information about potential nest sites may be advantageous in speeding up migrations, but could become counter-productive if it results in a suboptimal choice being made (Stroeymeyt et al. 2011b). Our results show that Pharaoh's ants are able to balance this trade-off. When provided with a familiar nest of poor quality and a novel nest of superior quality, the ants initially migrated primarily to the former, but then redirected traffic towards the superior nest. Pharaoh's ants are known to rapidly explore and assess novel ground in order to extend their foraging trails (Sudd 1960; Fourcassie and Deneubourg 1994). This exploratory behaviour may also be beneficial in house hunting if a better quality nest is available.

The use of colony-level 'memory' of potential nest sites may allow a more rapid migration, as demonstrated in *Temnothorax* (Stroeymeyt et al. 2010, 2011a), thus reducing the exposure of colonies to predators and the environment. Information is retained on poor nest sites to be avoided in *Temnothorax* ants (Franks et al. 2007) and on nest sites to be utilised in Pharaoh's ants. Pharaoh's ants can upgrade nest site mid-migration and *Temnothorax* ants show some similar abilities (Franks et al. 2008), while honey bees migrate to a temporary site initially before deciding on their final site (Seeley and Buhrman 1999, 2001). The decision making process in social insects, including the use of colony-level 'memory', is therefore adaptable and able to balance the need for speed with the slower process of finding the optimum solution.

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