



Parsimonious use of foraging pheromones during nest migration in ants

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Decision making is vital to the fitness of all animals, with many social species making consensus decisions that require efficient communication. Chemical signals are the most important tools for many animals, and are used notably by social insects in a wide variety of contexts, from foraging for food to recognition of nestmates. However, chemical cues may be biosynthetically limited and costly to produce, making their use in multiple contexts potentially beneficial. In this study we examined the role of foraging pheromones during nest migrations in the Pharaoh's ant, *Monomorium pharaonis*. Using a Y-shaped bridge apparatus, we tested whether ants would prefer migrating to a novel nest site along branches coated with attractive foraging pheromones rather than to a nest site reached via a control branch. We found that ants preferred to migrate to nest sites reached via branches with attractive foraging pheromones, and that there were more queens and workers in those nests at the end of the migration than in nests at the end of control branches. The results show that attractive foraging pheromones are utilized during nest migrations in the Pharaoh's ant, highlighting the evolutionary pressure to use signals in a parsimonious manner to improve communication during decision making.

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Group consensus decisions are characteristic of self-organization in eusocial species such as social insects, with group-level response being achieved by individuals responding to local stimuli governed by a simple set of rules (Bonabeau et al. 1997; Pratt et al. 2005; Boomsma & Franks 2006). In ants, decisions can be made on an individual level but often require colony-level participation, for example foraging for food, defence against predators and migration to a new nest site (Couzin et al. 2005). Information transfer is vital in these circumstances, and is transferred from informed to uninformed individuals through various mechanisms, to recruit these uninformed individuals to a resource (Billen 2006). This creates a positive feedback loop by exponentially increasing the number of individuals making a certain decision when a quorum threshold is reached (Pratt et al. 2002; Sumpter & Pratt 2009). Whether this decision is in the context of foraging, mate selection, nest site choice or avoidance of predators, efficiency in decision making should be maximized in order to improve the individual's or group's fitness (Krebs & Kacelnik 1993; Blumstein & Bouskila 1996).

A key task in many social insect societies is location and migration of the colony to a new nest site. Although nest migrations can provide many benefits to the participants, they can also inflict a number of costs and are often initiated under emergency conditions (Visscher 2007). Costs include metabolic and energetic

stresses, increased predation and the possibility of not finding a suitable new nest site (Rankin & Burchsted 1992). Such mass movements rely heavily on a coordinated migration in which the destination and route have been identified. Nest choice is extremely important to any animal and, despite migration being costly and dangerous, the selection of a suboptimal nest will reduce the overall fitness of the colony (Bartholomew et al. 1988; Healey & Pratt 2008). However, aside from two well-studied species (Franks et al. 2002; Visscher 2007), the organization of nest migration is little understood. In the honeybee, *Apis mellifera*, scouts return to the current nest and 'dance' to communicate the finding of an alternative nest site (Britton et al. 2002), and in the rock ant, *Temnothorax albipennis*, key individuals lead the decision making process during nest migrations (Stroeymeyt et al. 2011). Rock ants use two distinct techniques to recruit fellow nestmates to a new nest site. Early in the nest migration the scouts use tandem runs to lead other workers to the new site, and as the migration progresses, the ants switch to social transports in which they simply carry colony members from the old nest to the new site (Pratt 2008). Recruitment methods generally involve positive feedback as recruited individuals go on to recruit yet more individuals, and successful migrations therefore rely on efficient communication (Jackson & Ratnieks 2006; Guttal & Couzin 2010).

In many species efficient communication is achieved specifically through the use of pheromones. Chemical communication is one of the most widespread forms of communication, occurring among bacteria, fungi, plants and animals (Wyatt 2003). The social Hymenoptera have evolved very advanced societies, characterized

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by efficient communication systems based on chemical cues (e.g. Green & Gordon 2003; Howard & Blomquist 2005; Billen 2006; D'Ettoire & Lenoir 2010). A typical ant worker is a walking battery of exocrine glands with more than 10 different secretory glands used in the production of chemicals to convey information, which include pheromones to both attract and repel other individuals (Hölldobler & Wilson 1990). However, the capacity to synthesize chemical compounds is biosynthetically finite and costly, potentially leading to strong evolutionary pressure to utilize single products parsimoniously for multiple purposes (Blum 1996; Steiger et al. 2011). For example, cuticular antidesiccation compounds are utilized parsimoniously for recognition in the social Hymenoptera (Howard 1993; Blum 1996; Greenfield 2002; Steinmetz et al. 2003; Howard & Blomquist 2005; D'Ettoire & Lenoir 2010). Despite the virtually ubiquitous use of pheromones as a communication tool in social insects, however, there is a surprising lack of studies on their role during nest migrations.

We examined the use of foraging pheromones during nest migrations in the Pharaoh's ant. These ants use multicomponent pheromone trails when foraging for food (Jackson & Ratnieks 2006; Jackson et al. 2007). A long-lived attractive pheromone marks out a network of trails in the ant's foraging territory (Jackson et al. 2004, 2006), which is then 'activated' by a short-lived attractive pheromone upon the discovery of a food source (Jeanson et al. 2003; Jackson & Ratnieks 2006). As more ants select a path and lay pheromone on it, the path becomes more attractive, creating a positive feedback loop (Detrain et al. 1999; Beekman et al. 2001). The use of pheromones during foraging in the Pharaoh's ant is well studied (Jackson et al. 2004, 2006; Robinson et al. 2005, 2008a, b; Jackson & Châline 2007), but the use of pheromones during nest migration has only recently been investigated (Evison et al. 2012). In this study we examined the use of foraging pheromones during nest migrations and assessed how they influence the characteristics of these migrations. We tested whether the long-lived and short-lived attractive pheromones used during foraging had a positive recruitment effect during nest migration. We also examined whether ants would initiate migration faster when presented with trails of the short-lived attractive pheromone compared to that of the long-lived attractive pheromone (Jeanson et al. 2003).

METHODS

We used 20 colonies of Pharaoh's ants, each containing approximately 700 workers, 10–12 queens, and brood of various stages. Colonies were maintained in plastic boxes (22 × 16 cm and 7 cm high), the sides of which were coated with Fluon to prevent the ants from escaping. Colonies were maintained at 27.5 ± 2.5 °C, 80 ± 5% RH, 12:12 h L:D cycle, on a diet of *Tenebrio* larvae, honey water and ant diet (Keller et al. 1989). Each colony was provided with an artificial nest, consisting of a plastic box (45 × 32 mm and 12 mm high) with an entrance hole (approximately 5 mm) and a lid, consisting of a small sheet of red acetate and a plastic lid (the size of the box) wrapped in silver foil. Nestboxes used during nest migration experiments were of a higher quality than those present in the holding boxes (made from the same-sized plastic boxes as holding nestboxes but wrapped in electrical tape so that the inside of the nest was dark), to encourage nest migration. Nest migrations were initiated by removing the lid of the nests. Experiments were conducted at the same time of day to avoid effects of circadian variation in ant activity. 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).

Pheromone Collection

Pharaoh's ants are unicolonial, without nestmate recognition, which allowed us to use a different colony (donor colony) to that being used during the nest migration trial (test colony) for pheromone collection. The donor colony was starved of sucrose solution for 72 h to increase their need to forage for sucrose during pheromone collection. A Y-shaped bridge apparatus was introduced into the holding box with one branch leading to a platform upon which was a sucrose feeder that contained 1 M sugar solution (to collect both the short-lived and long-lived attractive pheromones simultaneously) and another leading to an empty platform (to form a 'nontrail' control branch that would be only lightly marked by the ants). In addition, a separate control branch was placed in the foraging arena of each test colony, far from the food and water resources. Exposing the control branch to the ants in this way avoided them being treated as novel areas by the ants (which increases attraction), or contaminated with positive pheromones laid to food or water resources (Fourcassié & Deneubourg 1994). The undersides of all Y-bifurcation and branch materials were coated with Fluon to ensure that the ants would only travel along the upper surface of the apparatus. This set-up was left for 30 min to allow the colony to establish foraging trails along the branches and lay down the foraging pheromones. After 30 min, the apparatus was removed and all ants were returned to the holding box. The branches coated with attractive pheromones from the Y-shaped bridge apparatus, as well as the 'nontrail' control branches that led to an empty platform, were then each attached onto a clean Y-shaped bridge apparatus together with a control branch from the arena ready for experimentation. Trials assessing the effect of the short-lived attractive foraging pheromone (as well as the 'nontrail' control branches) commenced immediately after pheromone collection as the short-lived pheromone is highly volatile and evaporates quickly (Jeanson et al. 2003; Robinson et al. 2008b). Trials assessing the effect of the long-lived attractive pheromone commenced 45 min after pheromone collection to allow the short-lived attractive pheromone to evaporate, hence leaving only the long-lived attractive pheromone to be tested (short-lived attractive pheromone has no effect after 33 min; Robinson et al. 2008b).

Nest Migration Trials

The Y-shaped bridge apparatus was placed into the holding box of the test colony, with each branch leading to a novel nest site. To assess the attraction of each type of branch (coated with either short-lived or long-lived attractive foraging pheromones, or the 'nontrail' control branch) to the ants during the migration process, the numbers of ants passing a point 1 cm from the Y-bifurcation along each branch during 30 s (outward traffic only) and the branch choice of every individual arriving at the junction during 30 s were recorded. These recordings commenced after 2 min and were recorded every 4 min for 30 min. In addition to the assessments of the migration process via ant counts, we recorded at what time queen and brood movement commenced. Following the 30 min trial the bifurcation apparatus was removed and the number of workers and queens in each nest, as well as the presence of any brood, was recorded. This process was repeated for each of the 20 colonies for each of the three branch types, leading to a total of 60 trials.

Statistical Analysis

We analysed all data in R 2.14.1 (R Development Core Team 2012). All traffic and branch choice data were analysed using linear mixed-effect models fitted by maximum likelihood, implemented using the lmer function in the lme4 package (Bates &

Maechler 2010). We analysed the data in two ways. To assess differences in the response to the three branch types we first modelled proportion of ants on or choosing the test branch as a function of time (a continuous variable), and its interaction with branch type (short-lived or long-lived attractive pheromones, or 'nontrail' control branch), using a binomial error structure. We then modelled number of ants on or choosing each branch as a function of time, and its interaction with branch type (test or control). In each analysis we fitted colony as a random effect to account for the multiple observations during each trial, and we used the likelihood ratio test to generate *P* values. Models were checked for normality by plotting the residuals against the fitted values and for homogeneity of variances (Faraway 2006). We compared the number of workers and queens in each nest at the end of the trials using paired *t* tests, the number of trials in which brood was present in each nest using Fisher's exact tests, and the time of queen and brood movement during each trial using ANOVA as these data were normally distributed.

RESULTS

Pharaoh's ants preferentially migrated towards nests accessed via the branches coated with attractive foraging pheromones rather than to the control branches, either those that had been placed in the arenas or those 'nontrail' branches that had led to empty platforms (Fig. 1). There was a significant interaction between branch type and both the proportion of ants on, and choosing, each branch over time (branch traffic: $\chi^2_2 = 23.8$, $P < 0.001$; individual choice: $\chi^2_2 = 8.69$, $P = 0.013$; Fig. 1), indicating that the ants' migration characteristics varied depending on which type of branch the ants were exposed to during a nest migration. Both the branch traffic and the number of ants choosing each branch were significantly higher on the branches coated with attractive foraging pheromones compared to the control branches (short-lived pheromone traffic: $\chi^2_1 = 251.5$, $P < 0.001$; Fig. 2a; long-lived pheromone traffic: $\chi^2_1 = 69.8$, $P < 0.001$; Fig. 2c; short-lived pheromone choice: $\chi^2_1 = 194.5$, $P < 0.001$; Fig. 2b; long-lived pheromone choice: $\chi^2_1 = 59.0$, $P < 0.001$; Fig. 2d). However, there were no differences in either branch traffic or the number of ants choosing each branch when ants were presented with the 'nontrail' control branch that had led to an empty platform compared to the control branch that had been placed in the arena (traffic: $\chi^2_1 = 0.376$, $P = 0.540$; Fig. 2e; choice: $\chi^2_1 = 0.463$, $P = 0.496$; Fig. 2f).

There was no effect of branch type on the time of queen or worker movement (queen: $F_{2, 57} = 2.05$, $P = 0.138$; worker: $F_{2, 57} = 2.44$, $P = 0.396$; Fig. 3). However, the branch type did have an effect on the numbers of workers and queens, and presence of brood, following the nest migrations (Fig. 4). Nests at the end of the branches coated with both short-lived and long-lived attractive pheromones contained significantly more workers (short: $t_{19} = 10.1$, $P < 0.001$; long: $t_{19} = 6.89$, $P < 0.001$) and queens (short: $t_{19} = 15.6$, $P < 0.001$; long: $t_{19} = 11.2$, $P < 0.001$), and a higher proportion of brood (short: $P < 0.001$; long: $P < 0.001$) at the end of the migration period compared to nests at the end of the control branches. Conversely, there was no significant difference in worker or queen number, or brood presence, between nests at the end of the 'nontrail' control branches that led to empty platforms compared to nests at the end of the control branches that had been placed in the arenas (worker number: $t_{19} = 0.278$, $P = 0.784$; queen number: $t_{19} = 0.816$, $P = 0.424$; brood presence: $P = 1$).

DISCUSSION

Pheromones that were laid during foraging were used by Pharaoh's ants during nest migrations. When ants were forced to

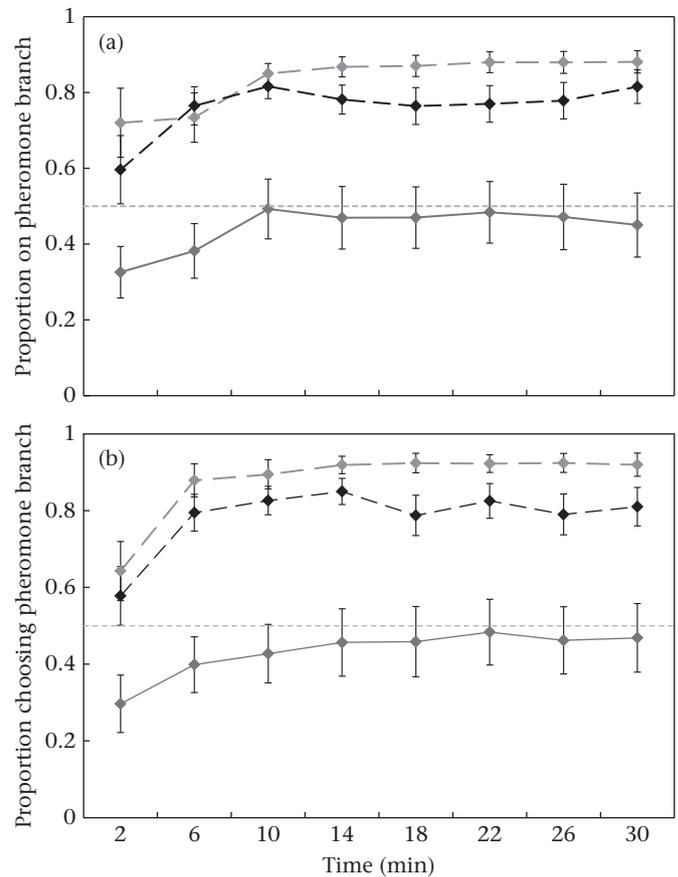


Figure 1. Mean \pm SE proportion of ants (a) counted on or (b) choosing the test branch as compared to the control branch during a nest migration. Grey dashed lines show the short-lived attractive pheromone branch, black dashed lines the long-lived attractive pheromone branch, and solid grey lines the 'nontrail' control branch that led to an empty platform. Dashed horizontal line at 0.5 represents the expectation if branch choice is random.

make emergency migrations, they preferentially migrated towards novel nest sites that were accessed via branches coated with attractive foraging pheromones. We also found more queens and workers, and a higher proportion of brood, in nest sites accessed via the attractive foraging pheromones compared to the control branches. Unexpectedly, however, there was no difference in the timing of key activities during a migration between the different types of pheromones we tested. It is clear from our experiments that ants are making use of attractive foraging pheromones during emergency nest migrations. The capacity to synthesize pheromonal compounds will be biosynthetically finite; therefore there is likely to be strong evolutionary pressure to utilize single products for multiple purposes (Blum 1996). Our study provides evidence of this parsimonious use of a key communication tool, pheromone trails, to improve efficiency in decision making.

We expected that ants would migrate faster to nests reached via the short-lived pheromone, as these are used to recruit individuals rapidly and to ephemeral resources (Jeanson et al. 2003; Robinson et al. 2008a), but we found no difference in migration times between any of the test branch types. This may be attributable to the forced nature of the migrations; nonemergency migrations may show a more distinct difference in timings of migrations. Alternatively, the lack of difference could be caused by the decay rates of the pheromones (Jeanson et al. 2003; Robinson et al. 2008b). Pharaoh's ants leave pheromone marks when exploring new territory and have also been suggested to leave repellent

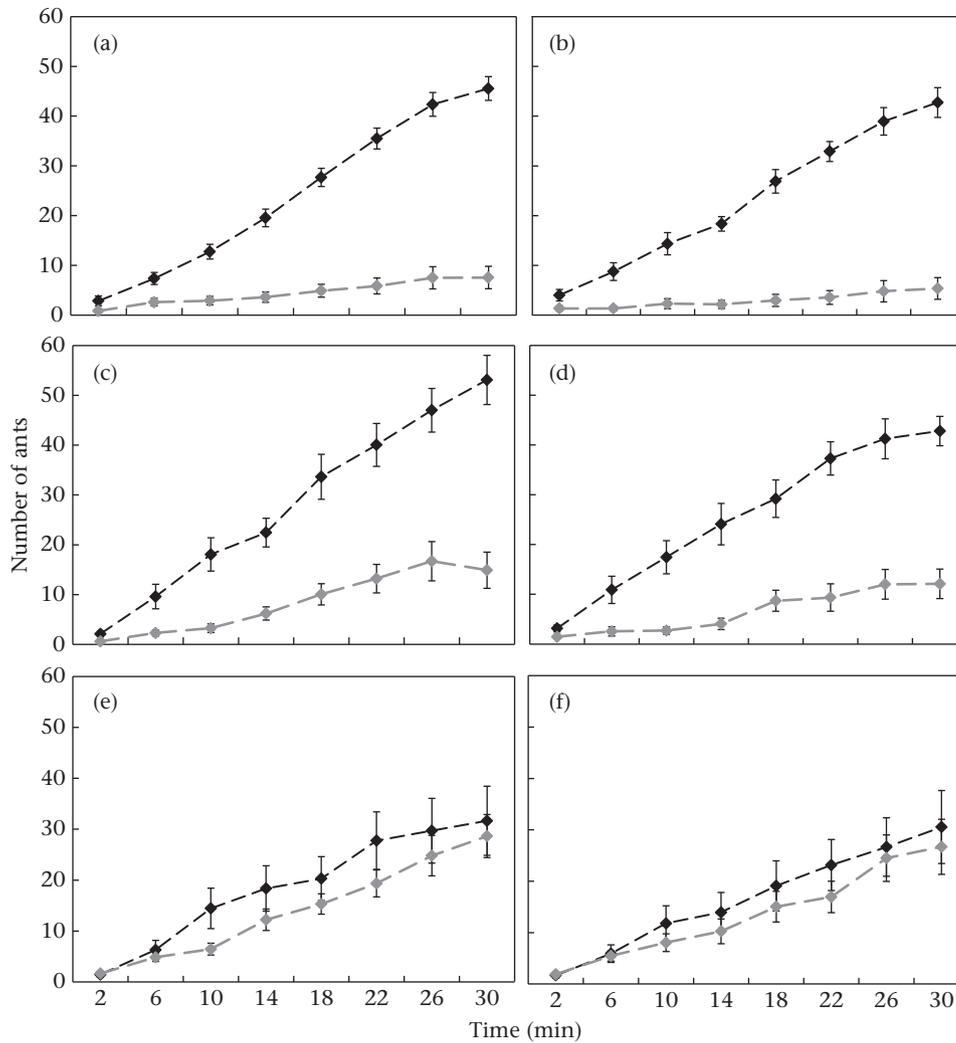


Figure 2. Mean \pm SE number of ants (a, c, e) on and (b, d, f) choosing either the test branch (black dashed lines) or the control branch (grey dashed lines) during a nest migration. (a, b) The short-lived attractive pheromone branch, (c, d) the long-lived attractive pheromone branch, and (e, f) the 'nontrail' control branch that led to an empty platform.

pheromones during foraging (Blum 1966; Fourcassié & Deneubourg 1994; Robinson et al. 2005), but the lack of effect of the 'nontrail' control branch that had led to an empty platform indicates that any such pheromone marks have no effect on nest migration. When

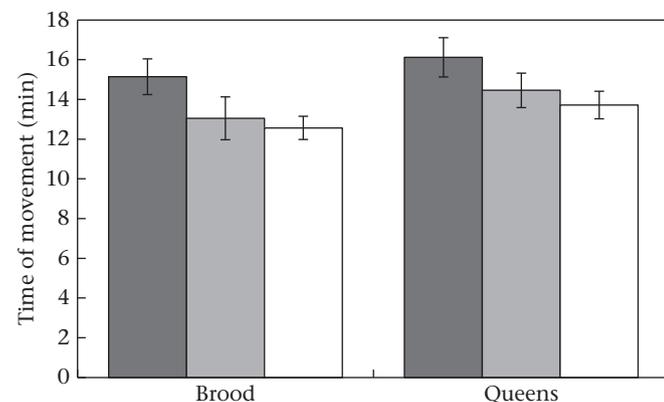


Figure 3. Mean \pm SE time of movement of brood and queens during a nest migration. Dark grey bars show migrations involving the short-lived attractive pheromone branch, light grey bars the long-lived attractive pheromone branch, and white bars the 'nontrail' control branch that led to an empty platform.

finding a new nest site it is important to find one that is suitable for the colony, as finding a suboptimal nest may present future complications (Bartholomew et al. 1988; Healey & Pratt 2008). Under emergency conditions, as in this study, this need is traded off with the requirement for speed (Stroeymeyt et al. 2010). It seems that the use of pheromones may mediate this trade-off by allowing ants to migrate to potentially familiar nest sites within the branching network of pheromone trails in their foraging territory (Jackson et al. 2004; Jackson & Ratnieks 2006; Dussutour et al. 2009; Evison et al. 2012).

The long- and short-lived attractive pheromones of Pharaoh's ants exhibited very similar effects to each other during migrations. It is likely that the long-lived pheromone is either a passively laid chemical, probably hydrocarbons from the footprints of the ants (Lenoir et al. 2009; Dussutour et al. 2009; Evison et al. 2012), or it may be a monomeric (Jackson et al. 2007) that is released at the same time that the ants actively lay the short-lived pheromone when they drag their gasters (Billen 1987; Jackson & Châline 2007). The result from either case is that the short-lived pheromone will be deposited in addition to the long-lived pheromone during foraging (Jackson et al. 2004; 2006). It is the long-lived pheromone that is most persistent in the foraging territory of this diurnal species of ant (Sudd 1960; Jackson et al. 2006), and it therefore seems most likely that the long-lived pheromone acts in a similar

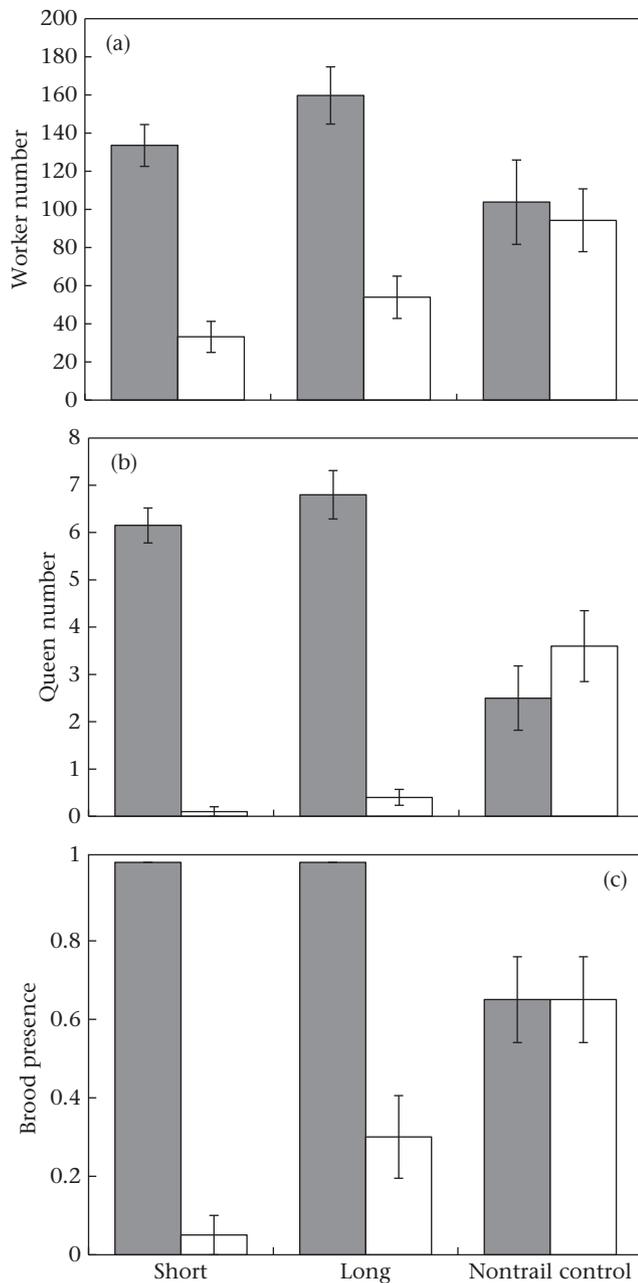


Figure 4. Mean \pm SE number of (a) workers and (b) queens inside nests, and (c) proportion of nests containing brood at the end of the nest migrations. Grey bars show nests at the end of the test branches, and white bars show nests at the end of the control branch.

way during nest migrations to its role during foraging (Jackson & Ratnieks 2006). The long-lived pheromone provides an initial guide trail that can be 'reactivated' with short-lasting recruitment pheromone once the migration is under way. As ants select the trail with long-lived attractive pheromone and lay short-lived attractive pheromone on it, a positive feedback reinforcement loop will be instigated, just as in the context of foraging. Our results suggest that the status of the long-lived foraging pheromone could be updated to an 'exploration' pheromone rather than a specific foraging pheromone (Dussutour et al. 2009). It seems likely that there may be parsimonious use of long-lived 'exploration' pheromones and short-lived recruitment pheromones in other ants as well. Army ants, for example, also use combinations of long-lived

and short-lived attractive pheromones during emigrations and foraging (Torgerson & Akre 1970; Chadab & Rettenmeyer 1975; Gotwald 1995; Billen & Gobin 1996), and, in the ponerine army ant *Leptogenys distinguenda*, a passively laid, long-lived attractive pheromone is used in both migrations and foraging, while a short-lived attractive pheromone appears more specific to foraging (Witte & Maschwitz 2001). Other ants too are thought to use pheromones during nest migrations (Mallon & Franks 2000; Tentschert et al. 2001; Blatrix et al. 2002; Buschinger 2010), and it will be interesting to discover whether the pheromones used are different from those used in foraging, or whether the same pheromones are generally used parsimoniously, as in the Pharaoh's ants.

Some of the strongest progress towards understanding the sociobiology of group decision making has been made with honeybees (Seeley et al. 2006; Visscher 2007), which use the same signal parsimoniously for foraging, nest site selection and migration in a way that parallels that found here in Pharaoh's ants. Honeybee colonies split via reproductive swarming, with the queen and approximately one-third of the workers migrating to a new nest site (Seeley et al. 2006; Visscher 2007). Scout workers direct their colony to this new nest site using the waggle dance that is best known for directing foraging, and the waggle dance is also used to direct bees during the migration itself (von Frisch 1967; Seeley & Morse 1977; Dyer 2002; Seeley & Visscher 2008; Seeley 2010). However, there are important differences between the dances used in the different contexts. When dancing for nest sites, the waggle dances are as precise as during foraging, with scouts also adjusting the strength of their dancing according to the site's value, although the way in which they adjust their dance differs between contexts. During migrations, in contrast, the dances are not precise, in particular with respect to distance information. While honeybees are therefore like Pharaoh's ants in using the same communication method parsimoniously for foraging and migrations, it appears honeybees may differ from Pharaoh's ants in modulating the composition of the signals according to context.

The ability to exploit a food source cooperatively or to move an entire colony to a new nest site are key characteristics of social organization, and the social Hymenoptera have elegantly developed the use of chemicals to improve communication during these processes (Morgan 2009). Just like the honeybee using its famous waggle dance parsimoniously in both contexts, we have shown here the parsimonious use of foraging pheromones in other contexts such as nest migration. This prudent use of signals in multiple contexts, particularly when they involve compounds that may be costly to produce, or signals that are complex to evolve, highlights the evolutionary pressures that shape efficient communication. Further investigation of the parsimonious use of signals is therefore likely to be valuable when investigating optimal decision making in animals.

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