

Queen location and nest site preference influence colony reunification by the ant *Temnothorax rugatulus*

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Abstract Social insect colonies adeptly make consensus decisions that emerge from distributed interactions among colony members. How consensus is accomplished when a split decision requires resolution is poorly understood. We studied colony reunification during emigrations of the crevice-dwelling ant *Temnothorax rugatulus*. Colonies can choose the most preferred of several alternative nest cavities, but the colony sometimes initially splits between sites and achieves consensus later via secondary emigrations. We explored the decision rules that govern reunification using artificially split colonies. When monogynous colonies were evenly divided between identical sites, the location of the queen played a decisive role, with 14 of the 16 colonies reuniting at the site that held the queen. This suggests a group-level strategy for minimizing risk to the queen by avoiding unnecessary moves. When the queen was placed in the less preferred of two sites, all 14 colonies that reunited did so at the preferred nest, despite having to move the queen. These results show that colonies balance multiple factors when reaching consensus, and that preferences for physical features of the environment can outweigh the queen's influence.

Keywords Consensus decision making · Nest site selection · Emigration · Queen · *Temnothorax*

Introduction

Group-living animals frequently confront decisions that require consensus on a single option (Camazine et al. 2001; Conrard and Roper 2005; Dyer et al. 2008; Kameda et al. 2012). This need is particularly clear for movement decisions, such as the choice of a new nest site by an emigrating ant or bee colony (Visscher 2007; Seeley 2010; Pratt 2010). While a colony may benefit from dividing among sites (Debout et al. 2007; Robinson 2014), the costs of separating the queen from part of her workforce include depriving her of their labor and might lower both queen and worker inclusive fitness.

Emigrating colonies possess effective means of achieving consensus, despite lacking well-informed leaders that can impose a single best choice on the entire group (Seeley 2010; Pratt 2010; Kaur et al. 2012; Cronin 2012). A decision instead emerges from competition among locally informed individuals, each of which promotes one option. The effectiveness of this promotion correlates with that option's quality (Seeley and Buhrman 2001; Mallon et al. 2001; Robinson et al. 2011). Quality-dependence does not by itself lead to consensus, but social insects have evolved additional mechanisms that do so, including quorum rules and highly nonlinear responses to recruitment signals (Pratt et al. 2002; Seeley and Visscher 2003; Pratt 2005; Sumpter and Pratt 2009; Cronin 2012). These tactics amplify differences in the popularity of competing options, so that recruitment to one site eventually dominates the others. Leaderless colonies can thereby cohesively move to a single site and also reach consensus in other contexts, such as foraging, escape from danger, and nest building by self-assembly (Nicolis and Deneubourg 1999; Camazine et al. 2001; Lioni and Deneubourg 2004; Altshuler et al. 2005; Pratt et al. 2005; Detrain and Deneubourg 2008; Seeley 2010; Cronin 2013).

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Consensus-building mechanisms are well illustrated by the emigration behavior of *Temnothorax* ants. These insects typically live in preformed cavities such as hollow nuts or rock crevices, and colonies are adept at emigrating to the best of several alternatives when their old nest is damaged or when a better site becomes available (Franks et al. 2002; Dornhaus et al. 2004; Pratt 2010). Decision-making relies on quality-dependent initiation of tandem run recruitment, in which a scout leads a single nestmate to a promising candidate home (Mallon et al. 2001; Robinson et al. 2011). Recruitment generates positive feedback through site population, and does so more effectively for better sites. The quality effect is amplified by a quorum rule under which slow tandem recruitment is succeeded by speedier social transport when a site population exceeds a threshold (Pratt et al. 2002). The winning site is likely to be the best one, because quality-dependent recruitment means that better sites attain a quorum earlier (Pratt et al. 2005; Pratt and Sumpter 2006; Sumpter and Pratt 2009). Once the ants accelerate migration by switching to transport, they are likely to complete the move before any competing sites reach a quorum.

While the ants' decision algorithm minimizes split decisions, it does not completely avoid them. Emigrating colonies sometimes transiently occupy multiple sites before reuniting at a single home (Franks et al. 2003a; Pratt and Sumpter 2006; Franks et al. 2008). These splits reflect a tension between colony cohesion and rapid movement, and they become more likely when dangerous conditions require a colony to move quickly (Pratt and Sumpter 2006; Franks et al. 2013). At a mechanistic level, splits occur when more than one site simultaneously attains a quorum, triggering social transport to multiple sites. Reunification requires a second stage of emigration in which all but one of the occupied sites are abandoned in favor of a single winner. The criteria that govern which site wins and the behavior that allows reunification of the colony remain poorly understood.

In this study we investigated the influence of two potential reunification criteria: The physical features of the occupied sites and the location of the queen. We expected that colonies should attend to site features, just as they do in the initial phase of emigration. Preference tests have shown that *Temnothorax* base their decisions on several factors, including entrance size, interior light level, and the height and area of the nest cavity (Pratt and Pierce 2001; Mallon et al. 2001; Franks et al. 2003b; Visscher 2007; Mitrus 2014). We further hypothesized that colonies prefer the site that holds the queen, to avoid moving her from one site to the other. Exposure during emigration is dangerous (Rettenmeyer et al. 1978; Franks and Sendova-Franks 2000; Dornhaus et al. 2004; Bouchet et al. 2013) and the queen's survival is vital to the colony's future fitness. *Temnothorax*

albipennis take special precautions to protect the queen; in migrations she is moved toward the middle of the emigration. This ensures that she always has the protection of roughly half of the colony's workers (Franks and Sendova-Franks 2000). It is, therefore, reasonable to expect that colonies might act similarly to minimize danger to the queen during reunification.

To investigate reunification, we split colonies of *T. rugatulus* between two sites and allowed them to reunite, noting which site they chose. To test for an effect of queen location we divided monogynous colonies between two identical nests and randomly assigned the queen to one of them. We then compared the relative influence of queen location and site design by placing these criteria in conflict; we divided colonies between two nests that differed in cavity brightness and placed the queen in the brighter, less preferred site. We subsequently observed the ants' choices to determine whether they weighed one criterion over the other. Queen number varies widely in *T. rugatulus* (Rüppell et al. 2001; Heinze and Rüppell 2014), but we focused on monogynous colonies, because we expected that protection of their only queen might be especially important.

Methods

Nest designs

Nests consisted of a 2.4 mm thick balsa wood slat placed between two glass microscope slides (50 × 75 mm). A circular hole drilled through the center of the slat created a 38 mm diameter nest cavity, accessible to the ants by a 2 mm wide slit through one side of the slat. To dim the cavity interior and make the nests more attractive to the ants, neutral density filters (Rosco Cinegel) were sandwiched between two microscope slides and placed on top of the nest. We used a single 1-stop filter in all nests except for the dimmer nests in the second experiment, which were fitted with three 3-stop filters. Balsa slats were discarded after each experiment, but slides were re-used after cleaning in a commercial dishwasher. See Sasaki et al. (2015) for further details on nest construction.

Subjects

The same 18 colonies were used in both the first and second experiments; an additional two colonies were used only in the second experiment. All colonies had a single queen, 50–150 workers, and 0–50 brood items. This size range is similar to that seen in other studies of nest-site selection by *Temnothorax* (e.g. Dornhaus et al. 2004; Robinson et al. 2009; Sasaki et al. 2015). Colonies were collected in the Pinal Mountains of Arizona (33.317N 110.876W) in May

and September of 2013 and 2014. Before the start of the experiments, colonies lived in nests like those described above but without the neutral density filters. Each nest was housed in its own 11 × 11 cm plastic box. Colonies were fed weekly with an agar-based diet (Bhatkar and Whitcomb 1970), and nest boxes were also provided with water tubes that were refilled weekly. Voucher specimens from each colony were deposited at the Arizona State University Natural History Collections in Tempe, Arizona.

Experiment 1: effect of queen

In this experiment we evenly divided each colony between two identical nests. We first placed the two nests into separate circular plastic arenas (24 cm diameter, 9 cm height), whose walls were coated with Fluon to prevent ants from escaping. The colony, still in its home nest, was placed into a third arena of the same design. We removed the roof of the home nest and waited 1–3 min, during which period some workers left the nest and wandered the arena. We took these ants to be the active scouts that find, assess, and recruit to candidate sites, while the passive majority of the colony waits at the old nest to be transported. We used soft forceps to evenly distribute the active ants, one-by-one, between the two target nests. We then similarly divided the ants that had remained within the nest, as well as the brood items. Pupae and larvae were moved one at a time using soft forceps. Eggs were too delicate to be grasped like this, but they would adhere to the tip of moistened forceps (or the head of an insect pin) gently pressed against them. In this way, clumps of eggs could be moved together. This approach ensured that each nest had a roughly similar balance of active scouts, passive ants, and brood. Finally, the queen was randomly assigned to one of the two nests, using Wolfram Alpha's virtual coin flip function (<http://www.wolframalpha.com>).

Colonies were given a few hours to move into their new nests, which were then placed in a single test arena with their entrances facing one another at a distance of approximately 6 cm (Fig. 1). The test arena, like those used to split the colonies, was first cleaned with ethanol to minimize cues that might bias the ants' decisions. Ants that were outside of the nests were also transferred to the test arena. Twenty hours later, we noted the nest at which the colony had reunited. A colony was described as reunified if at least four fifths of its members were found in one of the two nests. Reunification was also video-recorded with a Panasonic camcorder (HC-V520M) mounted on a copy stand approximately 60 cm above the arena. Colonies were split in the morning, and placed in the test arena in the mid to late afternoon.

On each day of the experiment, two colonies were tested simultaneously in identical setups placed adjacent to each

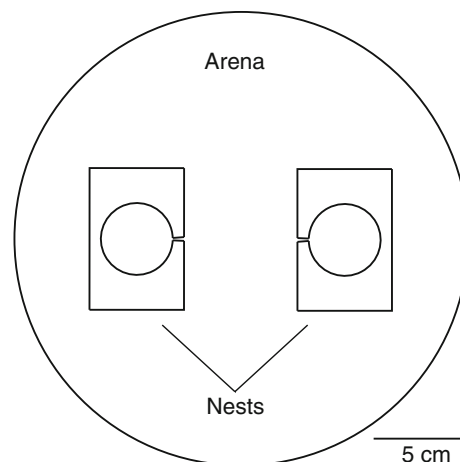


Fig. 1 Setup for reunification experiments. Colonies were evenly divided between two artificial nests placed approximately 6 cm apart in a circular arena

other on the same bench. In one member of each pair the queen was initially in the left nest, while in the other she was in the right nest. This controlled for any directional biases created by asymmetries of lighting or visual cues. Asymmetries were also minimized by performing the experiment in an environmental growth chamber evenly illuminated by overhead fluorescent lamps. If a colony was still split between the two sites at the end of observations, it was induced to reunify by removing the roofs of both sites and providing an intact third site nearby. In some cases, colonies that did not re-unite were re-tested at a later date, up to a maximum of three times. We waited at least one full day before re-testing a colony. This experiment was conducted in April 2015.

Experiment 2: effect of nest site design

In this experiment colonies were evenly split between two nests that differed in a physical feature known to influence the ants' site preferences. The nests were identical except for interior light level, achieved using three 3-stop filters in the roof of the better site versus a single 1-stop filter for the worse site [*Temnothorax* ants consistently prefer darker nests in choice tests (Franks et al. 2003b, 2006; Pratt and Sumpter 2006)]. The queen was always assigned to the brighter nest. Methods followed those of Experiment 1, except for the following differences: (1) instead of using forceps to divide each colony one ant at a time, we took an approximate count of the number of workers in each nest and then used a soft tipped paintbrush to split the ants roughly evenly between the two nests; (2) no colony was tested more than once, even those that failed to re-unite. This experiment was conducted in February and March of 2015.

Results

Experiment 1: effect of queen

Of the 18 colonies tested, nine reunited on their first trial, five on their second trial, and two on their third trial. The remaining two did not reunite, instead remaining roughly evenly split between the sites. Of the 16 colonies that reunited, 14 did so at the nest containing the queen, a significant preference (2-tailed binomial test: $p = 0.004$). If we consider the two non-reuniting colonies as being indifferent between the sites, we can assign one to each choice, giving a total of 15 for the queenright nest and three for the queenless nest. This still indicates a significant preference for the queenright nest ($p = 0.008$) (see Fig. 2).

Experiment 2: effect of nest site design

Of the 20 colonies tested, six did not reunite, instead remaining roughly evenly split between the sites, as in experiment 1. All of the 14 colonies that did reunite chose the darker, queenless nest over the brighter, queenright nest, a significant preference (2-tailed binomial test: $p = 0.0001$). As before, if we consider the six non-reuniting colonies to be indifferent, we can evenly divide them between the two choices, giving a total of 17 choices for the darker nest and three for the brighter nest. This pattern still indicates a significant preference for the darker nest ($p = 0.003$) (see Fig. 3).

Discussion

Monogynous colonies of *Temnothorax rugatulus*, when evenly divided between identical nests, reunited at the nest that contained their queen. This may be a group-level

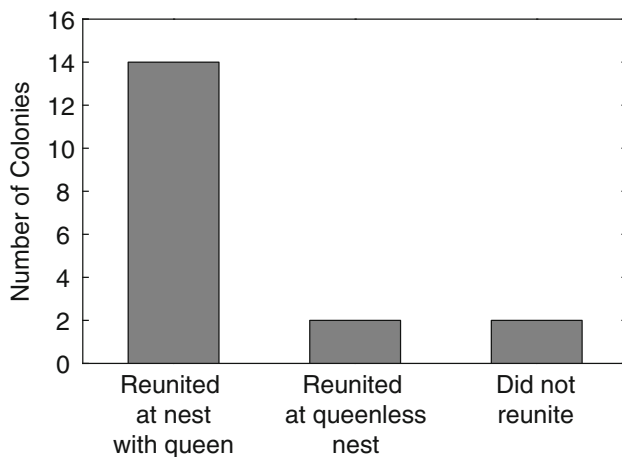


Fig. 2 Results of Experiment 1. Bar heights give the total number of colonies reuniting at the nest containing the queen, reuniting at the nest without the queen, or failing to reunite

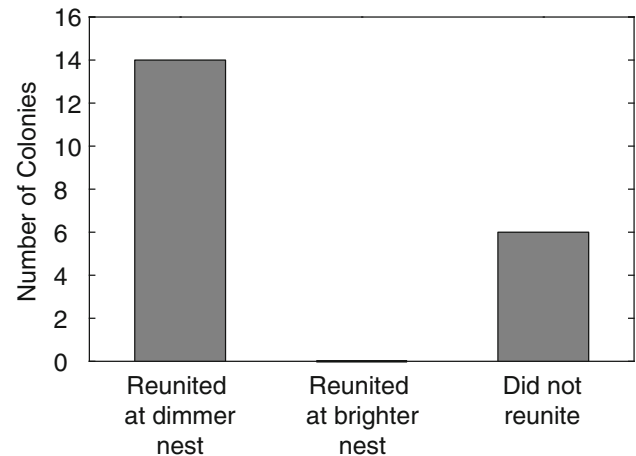


Fig. 3 Results of Experiment 2. Bar heights give the total number of colonies reuniting at the dimmer nest, reuniting at the brighter nest, or failing to reunite

adaptation for minimizing danger to the queen, whose egg-laying role makes a unique contribution to the entire colony's inclusive fitness. Colonies may benefit from a reunification strategy that minimizes the queen's exposure to potentially harmful environmental extremes and risks of predation. This behavior differs from that of the ponerine ant *Diacamma indicum*, for which the location of reproductive individuals did not determine where divided colonies reunite (Kaur et al. 2012). The reproductives of *D. indicum*, however, are not queens but gamergates, mated workers that can readily be replaced. A *T. rugatulus* colony that has lost its queen might also be able to rear a new one, as this species shows evidence of re-adoption of newly mated queens into their natal nests (Rüppell et al. 2001). Rearing a new queen takes weeks or months, hence these ants may be under stronger selection to protect the queen they already have. Similar selective pressures have been argued to account for the timing of queen movement by *T. albipennis* colonies, which typically bring her from the old nest to the new about halfway through the emigration (Franks and Sendova-Franks 2000). Movement earlier or later might increase the queen's risk of harm by leaving her behind in a nearly abandoned nest or moving her prematurely to a barely populated one. Like the decision rule reported here, this timing strategy may be a group-level feature that enhances the fitness of colony members. The selective importance of avoiding queen movement remains speculative until we can measure the actual risks to the queen at different phases of emigration.

The queen's location is not the only determining factor in reunification, as shown by our second experiment. When divided between two sites that differed in interior light level, colonies consistently chose the darker nest, even though this required them to move the queen from the brighter nest. The

functional consequences of a nest's light level on colony survival and reproduction are unknown, but previous observations make clear that *Temnothorax* colonies consistently prefer dimmer nests (Franks et al. 2003b). A reasonable assumption is that dimness is an indicator of site quality, because a dim cavity likely has a solid wall with few breaches and a small, defensible entrance (Franks et al. 2006). If so, we can interpret the choices we observed as a prioritization of long-term colony wellbeing over protection of the queen from a short-term risk. The optimal choice likely depends on the relative costs and benefits of each option. If faced with a small difference in site quality, the ants might do better by accepting a slightly inferior nest to minimize risk to their queen. Future experiments should test a range of quality differences to examine this possibility.

Queen location and nest dimness are not the only features likely to influence reunification. Ants show clear preferences for a range of site attributes, including cavity size and shape, entrance size, and contextual factors such as food availability and the presence of competitors, predators, or other hazards (Pratt and Pierce 2001; Franks et al. 2003a, b, 2007; Evison et al. 2012; Cao and Dornhaus 2012; Minter et al. 2013; Enríquez et al. 2013; Sasaki et al. 2014; Pontieri et al. 2014). Colonies somehow integrate these features when choosing among sites, and appear to weight them differently, presumably on the basis of their relative importance to nest function (Franks et al. 2003b; Sasaki and Pratt 2013). It is reasonable to assume that ants similarly attend to these attributes when reunifying after splitting between sites. In addition to the site features themselves, ants may be influenced by the distribution of colony members across sites. We took care to ensure that site populations were equal in our experiments, but differences are likely to arise in actual emigrations and may influence the ants' choice of where to settle. Colonies might benefit from choosing the most populous site, thus minimizing the number of ants that must be moved and exposed to external risks. Population could also serve as a symmetry breaker when sites are not otherwise well distinguished. Even with very simple rules, such as dependence of transport initiation on a site's current population, the colony could quickly amplify a small initial difference in population into consensus on a single site. Similar effects have been shown to account for collective selection of a single aggregation site (Jeanson et al. 2004, 2005).

Most of the colonies that we split reunited, but a portion did not, even after 20 h. These colonies might eventually have reunited if given more time, but their behavior can also be interpreted as a decision to remain separated. Reunification, like any migration, involves risks that colonies weigh when deciding whether to move. For example, when a colony is given the opportunity to move into a better nest, its probability of doing so depends both on the quality of its

current site and that of the new one (Dornhaus et al. 2004). If the improvement is too small, it will not justify the costs of emigration. Similar calculations may come into play during reunification, leading some colonies to avoid the costs of transporting half the colony to a new home. Division might have been favored in our experiments by the short distance between nests, which could make it easier for the two portions of the colony to remain in contact and function as a single entity.

Division also occurs in natural settings, either as a method of reproduction or as a strategy of seasonal polydomy. Several species of *Temnothorax* show evidence of polydomy (Alloway et al. 1982; Stuart 1985; Partridge et al. 1997; Roberts et al. 1999); in *T. albipennis* and *T. tuberum*, colonies appear to divide among multiple nests during the spring and summer, but reunite in a single nest over the winter (Partridge et al. 1997; Roberts et al. 1999). Polydomy can prevent overcrowding and enhance foraging efficiency during the growing season (Debout et al. 2007; Lanan et al. 2011; Cao 2013; Stroeymeyt et al. 2014; Robinson 2014). Reuniting at a single nest in winter can improve defense and environmental regulation during winter cold (Partridge et al. 1997; Roberts et al. 1999; Stroeymeyt et al. 2014). These seasonal shifts present another context, in addition to migration, where the ability to reunify may be important to a colony. In *T. rugatulus*, the occurrence of seasonal polydomy remains unexplored, but laboratory observations show that crowded conditions can induce colonies to divide among multiple nest sites (Cao 2013). Polydomy may also intersect with variation in queen number in this species. These ants are facultatively polygynous and possess two distinct queen morphs: larger macrogynes that disperse to found nests independently and smaller microgynes that are re-adopted into their natal nests (Rüppell et al. 2001). Variation among colonies in queen type and number are potentially associated with differences in reunification behavior. For example, polygynous colonies may be less sensitive to pressures to remain monodomous, and, when forcibly divided, we can speculate that they might reunite less frequently than monogynous colonies.

The findings reported here expand the study of colony emigration to the problem of reunification, a previously neglected aspect of consensus building. Temporary splits like the ones we created in the laboratory are likely to occur frequently in the life histories of ants, given the high frequency with which many species migrate (Hölldobler and Wilson 1990; McGlynn 2012). We focused here on the criteria that determine a colony's final choice of home, or whether to reunite at all. Another critical aspect of reunification is the behavioral mechanism by which colonies accomplish the challenging tasks of selecting a single site and coordinating the movement of their members to it. The same behavioral tactics that underlie emigration and

collective choice—including individual quality assessment, nestmate recruitment, and quorum rules—are likely to be important here as well, but other novel aspects of collective behavior may also come to light.

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