

The Effect of Brood Quantity on Nest Site Choice in the *Temnothorax rugatulus* (Hymenoptera: Formicidae)

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Subject Editor: Hongmei Li-Byarlay

Received 12 May 2020; Editorial decision 21 June 2020

Abstract

Ant colonies are self-organized systems, meaning that complex collective behavior emerges from local interactions among colony members without any central control. Self-organized systems are sensitive to initial conditions, whereby small random effects are amplified through positive feedback and have a large influence on collective outcomes. This sensitivity has been well demonstrated in collective decision-making by ants that use mass recruitment via trail pheromones, where it is attributed to the highly nonlinear relationship between the amount of pheromone on a trail and its effectiveness at attracting recruits. This feature is absent in many species, such as the rock ant *Temnothorax rugatulus* (Emery) whose tandem run recruitment shows a linear relationship between effort and effectiveness. Thus, these ants may have other behavioral responses that amplify initial differences during collective choices. We investigated this by testing whether nest site selection is influenced by small differences in the amount of brood at competing sites. Our results show that *T. rugatulus* colonies prefer a nest containing brood items to an empty nest, even when the brood-containing nest has only one brood item. When both nests have brood, colonies prefer the nest that contains more. However, as the numbers of brood items becomes more similar, this preference becomes weaker. Moreover, the smaller the difference in brood number, the more likely are colonies to split between sites. We discuss potential behavioral mechanisms for the observed effect, as well as its implications for number sense in ants.

Key words: collective choice, numerical cognition, quorum sensing

Ant colonies are self-organized systems, meaning that complex collective behavior emerges from local interactions among colony members without any central control (Camazine et al. 2003, Detrain and Deneubourg 2006, Gordon 2010). One feature of self-organized systems is that collective outcomes are sensitive to initial conditions (Camazine et al. 2003, Sumpter et al. 2012). For example, when a colony of the garden ant, *Lasius niger*, is given two bridges that are equidistant to a food source, scouts use both bridges, but random differences mean that one bridge will be used slightly more than the other one. This initial bias is amplified through pheromone trail recruitment—slightly more pheromone is initially laid on the ‘preferred’ bridge, thus attracting more scouts, who in turn reinforce the trail so that it attracts even more scouts. Eventually, this positive feedback leads to symmetry breaking: the colony predominantly uses one bridge over the other, even though both are identical (Beckers et al. 1992a, b). A similar pattern has been observed during nest-site choice in *Myrmecina nipponica* ants that also use trail pheromones for recruitment (Cronin 2013).

Symmetry breaking by mass-recruiting ants depends on the nonlinearity of their recruitment, in which a small increase in trail pheromone leads to a disproportionate increase in trail effectiveness. This feature quickly amplifies small initial differences in the strength of trails to competing options. However, not all social insect recruitment has this quality. The honey bee dance language and tandem recruitment by *Temnothorax* ants, for example, have a linear relationship between recruitment effort and number of recruits (Detrain and Deneubourg 2008, Shaffer et al. 2013). Thus, doubling the number of dance circuits or tandem runs roughly doubles the number of recruits obtained, in contrast to the greater than doubling seen for pheromone trails. Models suggest that such linear systems will not break symmetry, and this prediction has been confirmed for *Temnothorax rugatulus* (Emery) colonies presented with two equal sucrose feeders (Lanan et al. 2012, Shaffer et al. 2013). Rather than focus their effort on a single feeder, *T. rugatulus* colonies divide their foragers roughly equally between the feeders.

Although linear recruitment does not create symmetry breaking, species that rely on it may have other mechanisms that create sensitivity to initial conditions. Such mechanisms would be especially useful in contexts where consensus is important. This may not be the case for foraging by *Temnothorax*, but it is likely to be true for nest site selection, when a colony will generally benefit from moving all of its population to a single place. Here, we ask whether nest choices are sensitive to small differences in the number of brood items in two competing nest sites that are otherwise identical. Such small differences could arise randomly in the course of an emigration, and thus are a good candidate for a cue that helps the colony to reach consensus.

The emigration process of *Temnothorax* colonies is well documented (Mallon et al. 2001, Franks et al. 2002, Pratt 2005a, Pratt and Sumpter 2006, Sasaki and Pratt 2018). *Temnothorax rugatulus* ants live in rock crevices and are adept at moving to a new home when their old one is damaged. At the start of emigration, scouts leave their old nest and look for a potential nest site. When a scout finds one, she assesses its quality based on features such as entrance size and interior light level (Franks et al. 2003). If the quality is good enough, she goes back to her old nest and recruits fellow scouts, one at a time, via tandem runs (Möglich et al. 1974). Once the population of the new site surpasses a threshold, or quorum, she switches from tandem runs to transport, physically carrying nestmates to the new site (Möglich and Hölldobler 1974, Pratt 2005b). Transport is faster and more stable than tandem recruitment, and it brings the passive majority of workers, as well as brood and queens, to the new site. When two target nests of different quality are presented, the colony usually moves entirely to the better site (Mallon et al. 2001, Franks et al. 2002, Pratt and Sumpter 2006). Models indicate that this is due to quality-dependent recruitment—the better the site, the more likely a scout is to recruit to it—and to the nonlinearity introduced by the quorum rule (Pratt et al. 2005, Pratt and Sumpter 2006). However, it is not clear whether these mechanisms are sufficient to generate consensus when options are very similar; hence, ants may have other behavioral responses that amplify random differences between sites.

In this study, we explore whether nest site choice is influenced by small differences in the amount of brood at each site. Such differences could arise by chance during emigration, and thus might play a role in breaking symmetry between sites. Because brood are important to the ants, we predicted that colonies would prefer a nest site containing brood items to an empty nest. Furthermore, we expected that, when both nests have brood items, colonies would prefer the one with more brood items and that this difference would depend on the difference in the number of brood at the two sites.

Materials and Methods

Subjects

We used 104 colonies of *T. rugatulus*. Colonies were collected from the Pinal Mountains near Globe, Arizona (N 33°19.00'N 110°52.56'W) on 3 August 2011, 11 March 2012, and 9 December 2012. Each colony was housed in a nest described like that shown in Fig. 1. Each nest was kept in an 11 × 11-cm plastic box with walls coated with a film of Fluon to prevent ants from escaping. Each box included a water tube and a tray of agar-based diet that were refreshed weekly (Bhatkar and Whitcomb 1970). Nineteen colonies were used twice (once in each experiment). Colonies were given at least 2 wk rest between experiments, to avoid any effects of emigration experience on performance. Previous work on another *Temnothorax* species found evidence for such effects but showed that they vanish after 1 wk of rest (Langridge et al. 2004).

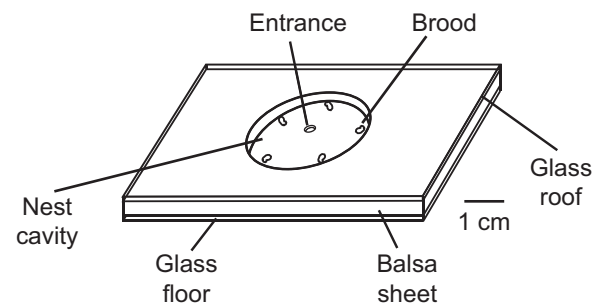


Fig. 1. A nest with five brood items. Each nest was constructed from a sheet of balsa wood (2.4-mm thick) with a central circular cavity (38-mm diameter) sandwiched between two glass microscope slides (50 × 3 × 75 mm) with a central entrance hole (diameter = 3.2 mm) drilled into the upper slide. Balsa slats were made fresh for each experiment and never re-used. Glass slides were re-used after washing in a household dishwasher.

Experimental Procedure

To test the effect of brood presence and amount on nest choice, colonies were presented with a binary choice between two target nests that were identical except for the number of brood items they contained (Fig. 1). Brood were manipulated with the head of a #2 insect pin (BioQuip, Rancho Dominguez, CA; Fig. 1), moistened to allow temporary adhesion and then gently applied to the brood. Brood items were evenly distributed along the periphery of the nest cavity; if there was only a single brood item, it was placed at any point along the periphery. The only type of brood used for placement was larvae (all stages), and the brood used in each test were from the subject colony.

To carry out the choice test, the home nest containing the colony was first placed against one wall of a rectangular plastic arena. Two target nests were then introduced against the arena wall opposite from the home (Fig. 2). To induce a migration, the glass roof of the home nest was removed and placed on the arena floor immediately in front of the nest. Nest-site preference was assayed by recording which sites were occupied by the colony 12 h later. If one site contained more than 90% of colony members, including all queens and brood items, we designated that as the colony's choice; otherwise the decision was categorized as split. Populations at each site were counted from photographs taken at the end of the experiment. Counts did not distinguish workers and brood items, and they excluded queens. Reported counts are probably underestimates, because clumping of colony members concealed some of them, especially in more populous nests. The raw count data are available as [Supp Material \(online only\)](#). All the experiments were conducted from June 2012 to March 2013.

Experiment 1: Do Colonies Prefer Nests With Brood Items to Empty Nests?

To test whether colonies prefer a nest containing brood to an empty nest, we gave colonies a binary choice: one nest seeded with five brood items and the other left empty. We further tested if even a single brood item influences colony nest preference using the same experimental design but placing only one brood item instead five in the target nest.

Experiment 2: Do Colonies Care About Different Amounts of Brood?

After observing that colonies preferred nests with brood, we tested whether colonies distinguish between nests with different amounts of brood. We gave colonies a series of choices between

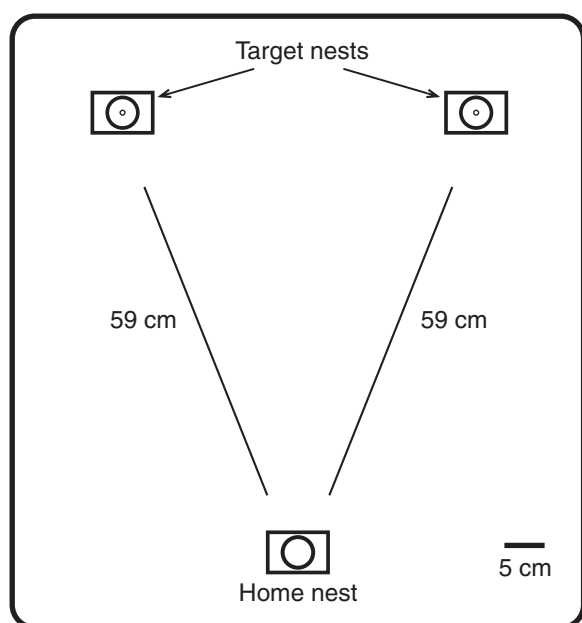


Fig. 2. Experimental arena. The home nest containing a colony was placed 7.0 cm from the short wall and 29.5 cm away from each of the longer walls in a rectangular plastic arena (60 × 76 cm). Two target nests were placed at the end of the arena opposite the home nest, each nest 10 cm from the wall, and the distances from the home nest to each target nest were identical (59 cm). The left/right positions of the two target nests were randomized across trials. The walls of experimental arenas were coated with Fluon to prevent the ants from escaping. Before each experiment, the experimental arena was cleaned with ethanol to remove any chemical marks left by the ants.

two target nests: a high-brood nest, which consistently held five brood items in all trials, and a low-brood nest, which held 1, 2, 3, or 4 brood items.

Analysis

Colony preference for each binary nest choice in experiment 1 was assayed using a two-tailed binomial test. In experiment 2, we used two different analyses to test the effect of the amount of brood items in the low-brood nest. To analyze the consensus dataset (only those colonies that moved into a single nest), we performed logistic regression with number of brood items in the low-brood nest as a predictor variable and nest choice as a dependent variable. To analyze the full dataset, including split decisions, we performed Kendall–Theil regression, a nonparametric form of linear regression (Gilbert 1987). To test the influence of differences in brood on the probability of splitting, we used logistic regression with number of brood items in the low-brood nest as a predictor variable and the occurrence of splitting as the dependent variable. The statistical software R (v. 3.5.1) was used for all analyses, and the ‘mblm’ function in the ‘mblm’ package was used for the Kendall–Theil regression.

Results

Experiment 1

Given a choice between a 5-brood nest and an empty nest, 19 out of 24 colonies chose the 5-brood nest (Fig. 3a; two-tailed binomial test: $P < 0.01$). Even when only one brood item was placed in a nest instead of five, 14 out of 17 colonies still preferred the nest with brood over the empty nest (Fig. 3b; two-tailed binomial test: $P = 0.01$).

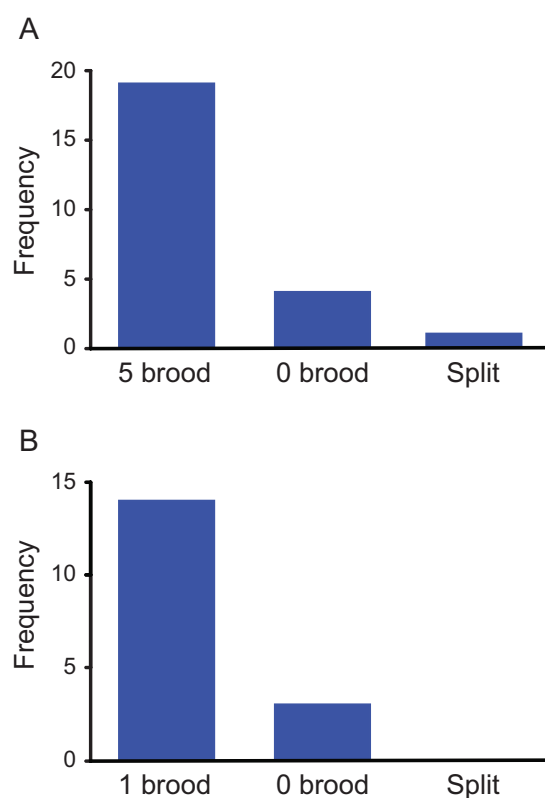


Fig. 3. Choices between (a) a nest with five brood and an empty nest ($n = 24$ colonies) and (b) a nest with one brood and an empty nest ($n = 17$ colonies).

Experiment 2

We analyzed the ants’ preferences between a high-brood nest (holding five brood items in all trials) and a low-brood nest (holding fewer than five brood items). The data for trials with zero items in the low brood nest were taken from experiment 1 (Table 1). We first focused on consensus decisions by excluding the split choice outcomes (i.e., the right column data in Table 1). Our results showed that the high-brood nest was generally preferred to the low-brood nest, but this preference became weaker as the number of brood items in the low-brood nest increased (Fig. 4; logistic regression: $z = 3.23$, $P < 0.01$).

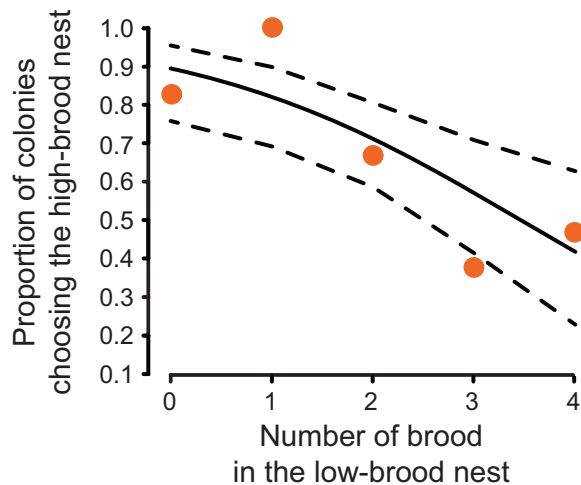
A large number of split decisions (37.6%; 47/125) was observed, and colonies split more often as the number of brood items in the low-brood nest increased (Fig. 5; logistic regression: $z = 2.39$, $P = 0.02$). To include these split decisions in our assessment of nest site preference, we re-analyzed the data using the proportion of colony members occupying the high brood nest site as our measure of preference. Consistent with the results for the consensus decisions, we found that preference for the high-brood nest weakened as the brood number in the low-brood nest grew closer to that of the high-brood nest (Fig. 6; Kendall–Theil regression: $F = 17.03$, $df = 1$, $P < 0.01$).

Discussion

Our results showed that *T. rugatulus* colonies preferred a nest containing brood items to an empty nest. Surprisingly, even when only one brood item was placed in a target nest, colonies significantly preferred this nest over the empty one. When both nests had brood items, colonies preferred the nest containing more brood items.

Table 1. Colony choices for each comparison test

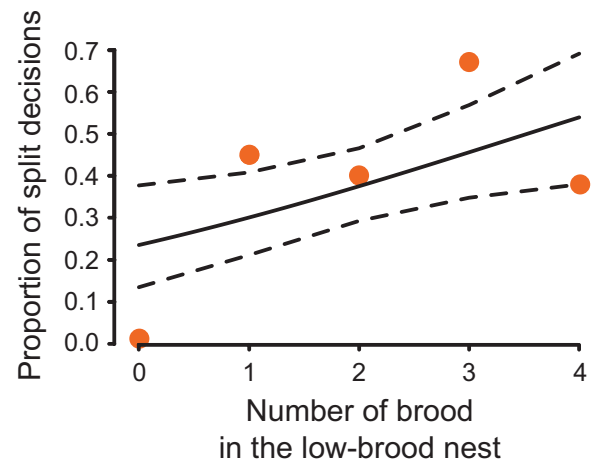
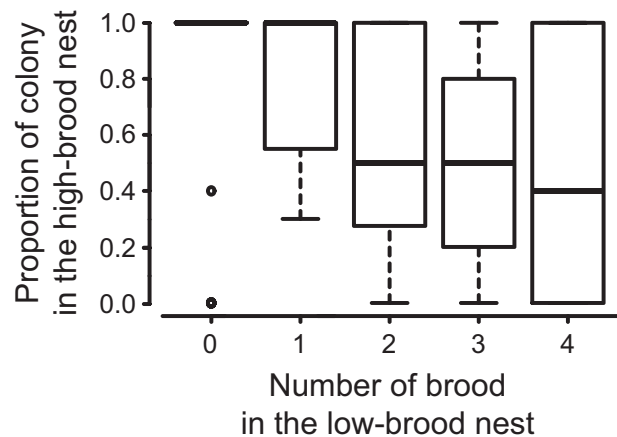
Number of brood items in the low-brood nest	Choice		
	High-brood nest	Low-brood nest	Split
0	19	4	1
1	17	0	14
2	10	5	9
3	3	5	16
4	7	8	7

**Fig. 4.** Proportion of colonies choosing the high-brood nest (5 brood items) over a low-brood nest (0–4 brood items). Plot shows only the ‘consensus’ data (i.e., at least 90% of colony members moved to either the high-brood nest or the low-brood nest). The solid line shows a fitted logistic regression model, and the dashed lines are 95% CIs.

However, as the numbers of brood items became more similar, this preference became weaker. Moreover, the smaller the difference in brood number, the more likely were colonies to split between sites.

How did the brood items in target nests affect collective choice? One possibility is that a nest with more brood items reaches quorum sooner than the competing nest. In other *Temnothorax* species with similar emigration behavior, scouts switch from slow tandem runs to faster transports based on the number of nestmates present in the site they are recruiting to (Pratt et al. 2002, Pratt 2005a,b). Because the nest containing more brood items had more nestmates, its quorum might be reached sooner, which could accelerate the start of transport and cause the whole colony to emigrate there. However, this possibility is discounted by the fact that a single brood item was enough to create a strong preference over a competing nest that was empty. Since the relationship between the number of nestmates in a nest and the probability of switching to transport is rather noisy (Pratt 2005b), it seems unlikely that only one brood item consistently helped colonies reach the quorum sooner.

Another possibility is that brood might count more strongly toward the quorum than an adult ant. That is, when a scout encounters brood in a target nest, she might be more likely to switch to transport than when she sees the same number of adults. This is plausible because brood items are usually transported later during emigration and are direct evidence that at least one other ant has started to

**Fig. 5.** Proportion of colonies splitting between a high-brood nest (5 brood items) and a low-brood nest (0–4 brood items). The solid line shows a fitted logistic regression model, and the dashed lines are 95% CI.**Fig. 6.** Proportion of colony members (workers and brood items) in the high-brood nest when colonies were given a choice between nests with high (5 items) and low (0–4 items) brood counts. Each box extends between the lower and upper quartiles, a horizontal line within the box indicates the median, and whiskers show the range of the data, except for outliers indicated by open circles.

transport to the site (Mallon et al. 2001, Franks et al. 2002, Pratt and Sumpter 2006). Thus, when a scout encounters brood, it is a good cue that other scouts have already committed to the nest site and that she should do so as well.

Presence of brood items could also influence behavior other than quorum sensing. For example, volatile chemicals released by brood might help scouts find the nest containing them. It is unknown from how far away *T. rugatulus* can smell their brood items, but ants are known to have an acute sense of smell in general (Hölldobler and Wilson 1990). For example, desert ants, *Cataglyphis fortis*, can smell dry biscuit crumbs from up to 3 m (Wolf and Wehner 2000). Thus, it is possible that *T. rugatulus* scouts were able to smell brood and orient toward it, thus enhancing the rate at which the brood-containing nest site was discovered. Furthermore, although it has been assumed that the presence and numbers of nestmates do not affect scouts’ nest site assessment (Pratt et al. 2005, Pratt and Sumpter 2006), brood might influence the probability that a scout accepts a nest and initiates tandem runs to it. Lastly, when scouts encounter

brood in a target nest, they might stay longer than when visiting an empty nest or a nest containing less brood. As a result, the population at a nest site would accumulate more quickly and reach the quorum sooner. In short, the relationship between presence of brood items and the behavior of scouts remains unclear, and these possibilities must be carefully tested in future studies.

One may wonder if our results show that ants are capable of counting because scouts were able to choose the nest site with a larger number of brood items. Although the ability to count was believed to be unique to humans (Nieder 2005), it is now known that species across many taxa can discriminate the number of objects (Dehaene 2011). In fact, some ability to count has already been shown in honeybees (Pahl et al. 2013). They can count up to four objects (Dacke and Srinivasan 2008) and also understand the concept of zero, which is a rare ability in nonhuman animals (Howard et al. 2018). To discriminate the numbers of brood items in nest sites in our study, however, scouts need not be able to count. They could simply measure continuous variables that correlate with the number of brood items, such as total surface area or the strength of brood odors, and still choose the nest containing more brood. In fact, a past study on another *Temnothorax* species showed that colonies can discriminate target nests with different numbers of entrances—colonies consistently choose a nest with fewer entrances—but, it turns out that they can achieve this using a continuous variable, the interior light level (Franks et al. 2006).

Our results also do not demonstrate that scouts have the ability to compare numbers of objects, another important numerical skill (Dehaene 2011). *Temnothorax* scouts typically visit only one nest site even when multiple sites are available (Sasaki and Pratt 2011, 2012), and the collective choice emerges from a complex communication network among colony members (Pratt 2005a, Valentini et al. 2020). Therefore, most of the scouts in our study did not have an opportunity to directly compare brood items in nest sites. In sum, although our findings seem to suggest numerical skills in ants, our data are insufficient to claim so. It is increasingly clear that experiments have to be very carefully designed in order to demonstrate numerical skills in animals (Shettleworth 2009, Nieder 2020). Future research can apply to ants experimental designs that have already been used to test numerical skills in other insects (Pahl et al. 2013). For example, researchers can test if psychophysical laws, such as Weber's law, hold for the numerical representations of ants (Cronin 2014, Reina et al. 2018, Nieder 2020).

Our study shows that collective decision making in *T. rugatulus* colonies is sensitive to initial conditions, as in other social animals (Camazine et al. 2003, Gordon 2010, Seeley 2010, Sumpter 2010). To our best knowledge, this is the first study showing that presence of brood items affects nest choice in ants. To decipher the underlying mechanism of this collective decision making, it is important to understand complex communication networks and behavioral algorithms at the individual level. Because movement of individual *Temnothorax* ants and interactions among them are relatively easily measured (Mallon et al. 2001, Sasaki and Pratt 2018, Valentini et al. 2020), these colonies offer many advantages to study emergence of collective decision making, in particular how small changes in initial conditions dramatically affect collective outcomes.

Acknowledgments

We are grateful to Adam Cronin and one anonymous referee for helpful comments on the manuscript. This work was supported by Award 1012029 from the National Science Foundation.

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