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Flexibility of collective decision making during house hunting in *Temnothorax* ants

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Abstract Many social animals cooperatively process information during decision making, allowing them to concentrate on the best of several options. However, positive feedback created by information sharing can also lock the group into a suboptimal outcome if option quality changes over time. This creates a trade-off between consensus and flexibility, whose resolution depends on the information-sharing mechanisms groups employ. We investigated the influence of communication behavior on decision flexibility in nest site choice by colonies of the ant *Temnothorax rugatulus*. These ants divide their emigration into two distinct phases separated by a quorum rule. In the first phase, scouts recruit nestmates to promising sites using the slow method of tandem running. Once a site's population surpasses a quorum, they switch to the faster method of social transport. We gave colonies a choice between two sites of different quality, and then switched site quality at different points during the emigration. Before the quorum was met, colonies were able to switch their choice to the newly superior site, but once they began to transport, their flexibility dropped significantly. Close observation of single ants revealed that transporters were more likely than tandem leaders to continue recruiting to a site even after its quality was diminished. That is, tandem leaders continued to monitor the quality of the site, while transporters instead fully committed to the site without further assessment. We discuss how this change in commitment with quorum attainment may enhance the rapid achievement of consensus needed for nest site selection, but at a cost in flexibility once the quorum is met.

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Introduction

Among the advantages of group living is the potential to improve decision making through the collective processing of information (Krause and Ruxton 2002; Sumpter 2010). Individuals within a group have access to social information gained from other group members; this asset is especially useful if obtaining information is difficult or costly. For example, in an environment where food items are sparsely distributed, it will take a long time for a single individual to find all options. When many individuals search together, however, they can collectively discover all surrounding food relatively quickly. Moreover, by sharing information, the group as a whole can discriminate among options of different quality and concentrate on the best one (Conradt and Roper 2005;

Dyer et al. 2008; Sumpter et al. 2008; Sumpter and Pratt 2009).

In some circumstances, however, social-information use can have negative effects on decision accuracy. If individuals match the behavior of the group regardless of their own personal perspective (i.e., individual information), this can lead to an "information cascade" that drives all group members to a suboptimal choice (Giraldeau et al. 2002; Rogers 2003). This is particularly an issue in an unstable environment where a group can get locked into an option even after its quality has been depleted or a better option has become available. Avoiding this "lock-in" depends on how group members combine their own individual information about the environment with social information garnered from others (Beckers et al. 1990, 1992; Granovskiy et al. 2012). Relying too much on individual information can slow down decision making, but relying too much on social information can lead to a suboptimal choice due to inflexibility in the face of changing conditions. Thus, groups must balance a trade-off between the speed of their decision-making and its accuracy (Franks et al. 2003a; Chittka et al. 2009) or value (Pirrone et al. 2014).

How species resolve the tension between speed and flexibility depends on the information sharing mechanisms they employ. In the eusocial insects, where natural selection has shaped highly integrated behavior, there is wide variation in the recruitment behavior that colony members use to share information (Beckers et al. 1990; Seeley et al. 1991; Sumpter and Beekman 2003; Detrain and Deneubourg 2008; Grüter et al. 2010; Sumpter 2010; Granovskiy et al. 2012; Jeanson et al. 2012; Dussutour and Nicolis 2013; Cronin 2013; Grüter and Leadbeater 2014). Recruitment signals allow individuals to direct nestmates to promising food sources or nest sites; these recruits may recruit still others, generating positive feedback that can focus the colony's workforce on the most profitable option (Detrain and Deneubourg 2008; Jeanson et al. 2012). In a recent study (Latty and Beekman 2013), a range of ant species using different recruitment methods were offered two food sources whose relative quality was switched midway during exploitation. Those species that deployed foragers more rapidly to the initially better option were less able to change their choice after the qualities were reversed. This result suggests that recruitment systems that spread social information faster lead to lower flexibility. This pattern, however, might instead be due to other differences among these ant species, such as colony size (Latty and Beekman 2013). In this study, we addressed the relationship between information sharing and flexibility in a single ant species that shows a marked change in the speed of recruitment behavior over the course of decision making. We also looked closely at individual behavior to determine whether the acceleration of information sharing is associated with a change in how recruiters balance individual and social information.

Temnothorax rugatulus readily emigrate after destruction of their fragile rock crevice nests and effectively discriminate among multiple new nest options. Over the course of an emigration, they change the speed at which nestmates are informed of the new nest by switching between two recruitment methods. Scouts first recruit via tandem running, in which a successful worker leads a single recruit all the way to the site she has found (Möglich et al. 1974; Richardson et al. 2007). Once the population of a candidate site surpasses a certain number, or quorum, the scouts switch to carrying their nestmates, one at a time, to the new site. Because transports are much faster than tandem runs, site population growth accelerates sharply once a site reaches a quorum. This pattern suggests division of the emigration into a slow deliberative period, characterized by tandem recruitment of scouts, and a rapid execution phase in which the colony fully commits to the first site to reach a quorum (Franks et al. 2002; Pratt et al. 2002; Pratt 2005a). If so, the quorum may also mark a loss of flexibility, as the scouts cease tandem running and thus the possibility of readily re-directing their efforts to a later-discovered better site. In a foraging context, where only tandem runs are used, colonies show high flexibility, meaning that they can redirect scouts to a better option when relative food quality changes (Shaffer et al. 2013). During house hunting, we predict similar flexibility before the quorum is met, but a marked loss of flexibility afterwards.

Prior work on *Temnothorax albipennis* showed that colonies could successfully choose a superior nest that became available only after they had already started transporting to a worse site (Franks et al. 2007). This flexibility was limited, however, with only one quarter of colonies in the better nest even after 24 h. Because those experiments tested colonies at only one phase of emigration, it remains unknown how flexible colonies are during the tandem run phase, whether flexibility changes after quorum attainment, and how any changes might emerge from changes in the behavior of recruiters.

To measure decision flexibility over the course of emigration, *T. rugatulus* colonies were made to choose between two candidate nest sites unequal in quality. At different stages of the emigration, both before and after quorum attainment, the quality of the sites was switched. Flexibility was measured as the colony's success in moving to the newly superior site. Additionally, we performed a second experiment to determine whether any decline in flexibility could be explained by changes in individual recruitment behavior.
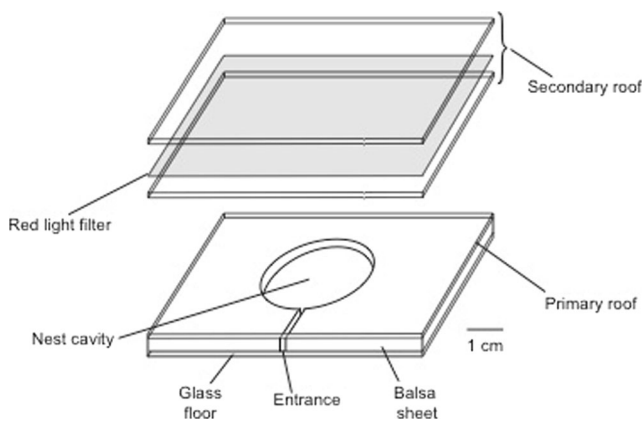
Methods

Subjects

We used 68 colonies of *T. rugatulus* (48 for experiment 1 and 20 for experiment 2). All had at least one queen, with worker

populations ranging from 110 to 185 and brood populations ranging from 50 to 200. Colonies were collected in the Pinal Mountains near Globe, Arizona (N 33° 19.00′, N 110° 52.56′, W). They were housed in nests like those described below but lacking a secondary roof. Each nest was kept in a lidded plastic box (11×11 cm), the walls of which were coated with Fluon to prevent the ants from escaping. Each box was provided with a water-filled plastic tube capped with cotton and an agar-based diet that was refreshed weekly (Bhatkar and Whitcomb 1970). All colonies were used only once.

Nest designs

In each experiment, colonies were induced to choose between a good and a poor nest. Both nest types were composed of glass microscope slides (50×75 mm) above and below a balsa wood slat (Fig. 1). In the center of the slat was a circular cavity at 4 cm in diameter, accessible to the ants through an entrance tunnel at 2.5 mm wide and 4.0 mm long. Atop each nest was a secondary roof, composed of two glass slides. For the good nest, a transparent red filter was inserted between the slides of the secondary roof to darken the nest interior. No filter was inserted for the poor nest. This was expected to make the good nest more attractive to the ants, who strongly prefer dimmer nests (Franks et al. 2003b; Pratt 2005b). A transparent filter was used to allow observation of scouts inside the nest interior. Red color further darkened the nest from the ants' perspective because ants have low visual sensitivity to red light (Briscoe and Chittka 2001). The secondary roof allowed us to switch the light filter between nests with minimum disruption to the ants.
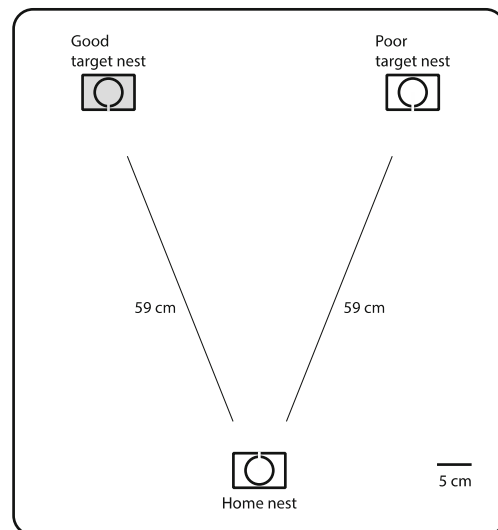
Experiment 1: decision-making flexibility by migration phase

To measure the colonies' baseline accuracy, we first had them choose between the good and poor nests without switching their quality. A home nest containing a colony was placed in a fiberglass arena (60×76 cm), 7 cm from the shorter wall and equidistant from the longer walls (Fig. 2). Target nests, one good and one poor, were simultaneously placed on the opposite end of the arena, 10 cm from each wall. Each target nest was 59 cm from the home nest. To induce emigration, the glass roof of the home nest was removed and placed on the arena floor immediately in front of the nest. The experiment was ended once no ants remained in the home nest, and the colony's choice was assayed by counting the number of ants in each target nest.

We then tested whether flexibility of decision making changes over the course of migration. The procedure was identical to that described above except that we switched the quality of the target nests at one of five distinct points. Because migration duration varies considerably among colonies, these points were based on stages of colony recruitment rather than time: 1st tandem run, 3rd tandem run, 5th tandem run, 1st transport, and 3rd transport. Once the ant performing the designated recruitment act reached the good nest, both secondary roofs were picked up simultaneously and exchanged. If any ants were on a secondary roof upon switching, they were removed and placed immediately next to the nest site. Once no ants remained in the original home nest, we ended the experiment and counted the number of ants in each target nest. Eight colonies were tested in each condition, but four had to be dropped from the analysis: two colonies that

Fig. 1 Nest design. Nests were constructed from a balsa wood slat with a circular cavity drilled through its center and an entrance tunnel on the side. The roof and floor were made of glass microscope slides. The primary roof was a single glass slide, fastened to the balsa slat with adhesive tape. The secondary roof was composed of two glass slides and was not fastened to the nest, to allow it to be easily removed and replaced during emigrations. For good nests only, a red filter was inserted in between the slides of the secondary roof

Fig. 2 Experimental arena. Colonies initially lived in the home nest, and its roof was removed to induce migration. Colonies were given a choice between two nests (good and poor) placed along the opposite side of the arena. The secondary roofs of each target nest were switched when the colony reached one of the pre-assigned migration milestones

had been assigned to the 3rd tandem run treatment switched to transport after only two tandem runs; two other colonies (one each in the 1st transport and the 3rd transport condition) recruited to the initially poor nest before the nest quality switch. This left a total sample of 44 colonies.

Before each experiment, the floor of the arena was cleaned using ethanol and tissue to reduce the influence of any chemical marks from past experiments. All experiments (including those described below) took place in the same location of the laboratory with consistent fluorescent lighting (450 lux).

Experiment 2: information usage by recruitment type

In this experiment, we measured the influence of recruitment type on recruitment persistence. We hypothesized that transporters would be more likely than tandem run leaders to continue recruiting to their original target nest even after its quality was diminished. That is, we expect transporters to have switched from deliberating the quality of the site to full commitment to it as the colony's new home. To test this, we traced the behavior of two kinds of recruiters: the 1st tandem leader and the 1st transporter. As in the first experiment, once the focal recruiter arrived at the good nest, we switched the qualities of the nests. We then followed the recruiter to investigate whether she continued to recruit or not. We tested ten colonies (one recruiter per colony) for each group.

To trace the behavior of a single recruiter, we recorded the migration using four video cameras: one took in the entire arena, while the other three recorded close views of the home nest, the good nest, and the poor nest, respectively. This thorough coverage allowed us to trace individual ants continuously, even when they were in crowded nests where the broad view of the arena camera could not distinguish them from nestmates. Once the focal recruiter was identified in the videos, we recorded if she continued to recruit to the formerly good nest after the nest qualities were switched. We labeled a recruiter as committed if she completed at least three additional recruitments to the originally good nest. If she did not recruit at all for 20 min after the switch, she was considered an uncommitted recruiter. An ant was also considered uncommitted if she completed one or two recruitments after the switch but then stopped recruiting for a 20-min period. Aside from the cameras, this experiment was set up identically to the first experiment. In past studies, ants typically have been uniquely painted in order to track them during migrations (Sendova-Franks and Franks 1993). However, because we had only one focal ant in each migration, the four-camera set-up was sufficient to track her.

Statistical analysis

In experiment 1, the aim was to determine if the flexibility of the migration was affected by the stage at which the nest quality switch occurred. Flexibility was measured by decision accuracy or the proportion of colony members in the newly superior nest at the end of migration. That is, a more flexible colony should be better able to redirect migration to the superior site after the switch. Accuracy lay between 0 and 1, with a value of zero meaning that all colony members ended the migration in the poor nest, while a value of one meant that they were all in the good nest. We used linear regression to detect an effect of migration stage on mean accuracy. Because migration stage is a categorical variable, we recoded it as a series of dummy variables so that it could be included in regression analysis. We also tested whether accuracy was influenced by colony size, measured as number of workers, number of brood items, total colony population, and the ratio of brood to workers, as previous research has shown that these factors can influence decision making (Donaldson-Matasci and DeGrandi-Hoffman 2013; Schaerf et al. 2013; Cronin and Stumpe 2014). Each colony size variable was included in the model to determine if it provided any additional predictive value compared with the model with migration stage only, and if not, it was removed from the model. We also fit another regression model in which migration stages were grouped according to recruitment phase (tandem run or transport). To evaluate the linear regression assumptions of normally distributed error, we performed Shapiro–Wilk tests on the residuals of the regression models. In experiment 2, we used Fisher's exact test to detect independence between recruitment behavior (tandem run or transport) and whether the recruiter continued recruitment after the nest quality switch. The statistical package Stata version 13 was used for all analyses. Significance was determined at the 5 % level.

Results

Experiment 1: decision-making flexibility decreases by migration phase

Migrations lasted from 5 to 9 h (median=6.3 h). Linear regression showed no significant effect of any of the colony size variables, hence we report results only for the effect of the stage at which quality was switched. When nest quality was not switched, colonies showed high accuracy; in seven of eight replicates, all colony members migrated to the good nest. The linear regression model showed that switching nest quality reduced decision accuracy ($F_{5, 38}=5.83$, $p=0.0004$) and did so more strongly with later switching points (Table 1; Fig. 3a). Switches during the transport phase generally led to lowest accuracy, with all transport stages significantly lower than both the no-switching case ($t_{38}=4.39$, $p=0.0001$; $t_{38}=3.56$, $p=0.001$; $t_{38}=4.06$, $p=0.0002$ for 1st, 3rd, and 5th transports, respectively) and the 1st tandem run ($t_{38}=2.91$, $p=0.006$; $t_{38}=2.08$, $p\leq0.044$; $t_{38}=2.57$, $p=0.014$ for the 1st,

Table 1 Summary of results for experiment 1

Treatment	Number of colonies	Average colony population	Average worker population	Average brood population	Median accuracy (%)	Minimum accuracy (%)	Maximum accuracy (%)
No switching	8	267	155	111	100	67	100
1st tandem	8	256	153	104	100	0	100
3rd tandem	7	322	158	164	50	33	100
1st transport	7	248	142	106	20	0	80
3rd transport	7	235	137	99	35	0	100
5th transport	7	251	146	106	40	0	67

Each row shows population statistics and accuracy achieved for colonies experiencing a nest quality switch at a particular migration stage

3rd, and 5th transports, respectively), which could not be distinguished from each other ($t_{38}=1.53$, $p=0.133$). Switching at the 3rd tandem run was intermediate, indistinguishable from either the 1st tandem run ($t_{38}=0.73$, $p=0.472$) or the 3rd ($t_{38}=1.31$, $p=0.198$) or 5th transports ($t_{38}=1.79$, $p=0.082$) but significantly different from the no-switching case ($t_{38}=2.21$, $p=0.033$) and the 1st transport ($t_{38}=2.12$, $p=0.041$).

When treatments were grouped by recruitment phase (tandem run or transport), linear regression showed that switching at either phase significantly reduced accuracy compared with the no-switching case (tandem: $t_{38}=2.20$, $p=0.033$; transport: $t_{38}=5.10$, $p<0.001$) (Fig. 3b). However, accuracy was lowest for switches during the transport phase, and significantly less than that seen in the tandem phase ($t_{38}=3.42$, $p=0.001$).

Fig. 3 Accuracy of decision-making for nest quality switches at different stages of migration. Accuracy is the proportion of ants in the good target nest at the end of migration. **a** Colonies that experienced no switching were highly accurate, but accuracy declined with later switch times. *Letters* indicate stages whose accuracy was not statistically distinguishable in pairwise comparisons ($p>0.05$). **b** When replicates were grouped by the phase of migration in which the switch occurred (tandem vs. transport), the two phases differed significantly from each other ($p=0.001$) and from the no-switching case ($p<0.05$). 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*
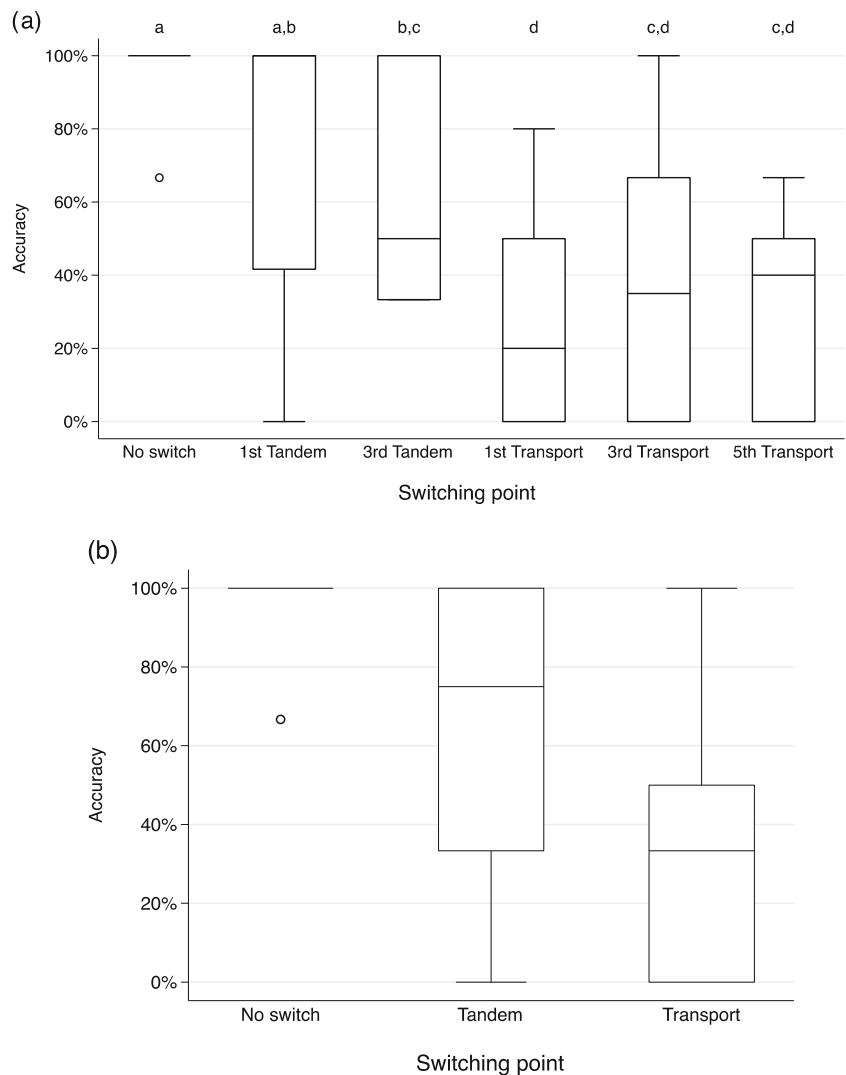
Neither the model with grouped treatments nor that with ungrouped treatments showed significant departure from the linear regression assumption of normally distributed errors (Shapiro–Wilk test, $p > 0.05$).

Experiment 2: transporting ants more likely to continue recruitment after switch

After the nest quality switch, ants that had begun transporting were significantly more likely to continue recruiting than were ants still leading tandem runs (Fisher's exact test, $p = 0.02$). Specifically, while 70 % of tandem runners stopped recruiting after the switch, only 10 % of transporters did so (Table 2).

Discussion

The results of our first experiment show that *T. rugatulus* colonies are more flexible in earlier phases of migration than later phases. Earlier work on *T. albipennis* suggested that colonies retain some flexibility even after transport has started (Franks et al. 2007). We found a similar result, but we further showed that flexibility during the transport phase was significantly lower than that seen in the tandem running phase. This finding accords with the idea that emigrations can be divided into an early deliberative phase and a later implementation phase, with the boundary marked by quorum attainment (Franks et al. 2002; Pratt et al. 2002; Pratt 2005a).

The standard for flexibility that we used was quite strict, in that the colony's decision was recorded as soon as the old nest was empty. Colonies that have split between sites at this point, or even moved entirely to the worse one, may eventually correct their error by mounting a secondary emigration to the better site (Franks et al. 2007, 2008; Doran et al. 2013). Indeed, such secondary moves may explain much of the flexibility reported by Franks et al. (2007), who assessed each colony's choice 24 h after the start of emigration. Given enough time, we expect that many of our colonies that chose the inferior site would similarly correct their choice. However, ignoring these secondary moves allowed us to better probe the colony's success in attaining an ideal performance in which

Table 2 Effect of nest quality switch on recruitment behavior

	Continuing recruitment	Stopped recruitment	Total
1st tandem runner	3 (30 %)	7 (70 %)	10
1st transporter	9 (90 %)	1 (10 %)	10
Total	12	8	20

Values in each cell give the number of individuals observed and percentage out of 20. While only 30 % of tandem run leaders continued to recruit to the originally good target after the nest quality switch, 90 % of transporters did so. The first tandem run leader and the first transporter showed significantly different behavior after the nest-quality switch ($N = 20$, $p = 0.02$)

initial consensus is reached on the best available site. Temporary splits and secondary moves likely impose costs in terms of energy, predation risk, and the possibility that splits will not be resolved. Our results show that these costs can only be reliably avoided when the best option is discovered before the onset of transport.

We further investigated the individual behavior underlying the observed change in collective flexibility. While tandem-running ants often abandoned recruitment after the quality of the target nest was depleted, transporting ants rarely gave up. Apparently, tandem leaders continue to monitor the quality of the site they are recruiting to, and thus can respond to changes that make it less attractive. Transporters, on the other hand, do not respond to these changes. This distinction mirrors earlier observations on how *Temnothorax curvispinosus* recruiters respond to changes in site population: after each recruitment act, tandem leaders assess target site population through their encounter rate with other ants, switching to transport once this information indicates that a quorum has been met (Pratt 2005a). When experimental manipulation prevents the site's population from increasing, tandem leaders often stop recruiting altogether (Pratt et al. 2002). Once an ant has begun transporting, on the other hand, she will continue to do so even after all the ants in the target nest are removed (Pratt 2005a). Our results show that transporting ants stop considering not only the number of ants in a target nest but also its quality. This change in behavior is consistent with recruiters switching from a deliberative state in which they remain open to nest site conditions, to an implementation state in which they simply carry out the emigration as fast as they can, regardless of changes at the site.

If tandem running is more flexible, why not use it throughout the emigration? The answer is likely that increased flexibility would be purchased at the cost of lower emigration speed. Tandem runs are roughly three times slower than transports (Pratt 2005b), making the latter a more efficient way to move the bulk of the colony's population. Recruiters might extend the period of flexibility by using a higher quorum, but this could lead to slower decisions and longer emigrations (Franks et al. 2003a; Pratt and Sumpter 2006). This tradeoff between the speed of decision-making and the probability of making the best choice is a fundamental one (Marshall et al. 2006; Chittka et al. 2009; Pirrone et al. 2014). In nature, it is very unlikely that features affecting nest quality (e.g., cavity volume and entrance size) change in a short period of time. Therefore, speed may be more valued than flexibility during nest site selection. This contrasts with foraging, where quality of options can quickly change and where ants rely exclusively on flexible tandem run recruitment. Thus, transportation behavior might have evolved to maximize speedy selection of the best option during house hunting.

Temnothorax colonies are known to adjust their emigration behavior to adaptively emphasize speed or accuracy. For

example, faced with nest destruction, harsh environmental conditions, or predators, ants may use a lower quorum as well as higher search and recruitment initiation rates to increase speed at the cost of accuracy (Franks et al. 2003a; Pratt and Sumpter 2006; Sasaki et al. 2013). Previous work has considered this tradeoff only in static environments, but our results suggest that colonies might also benefit by adjusting their behavior to environmental variability. However, it is still unknown if colonies in a fluctuating environment use a higher quorum threshold than ones in a stable environment. A recent study showed that *T. rugatulus* adjust their weighting of nest site attributes according to the local distribution of attribute qualities (Sasaki and Pratt 2013). Future research should investigate whether ants similarly adapt their quorum rule to the local stability of their environment.

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