ORIGINAL PAPER

Efficiency and regulation of recruitment during colony emigration by the ant *Temnothorax curvispinosus*

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Abstract Recruitment helps insect societies by bringing individuals to places where work needs to be done, but it also imposes energetic and opportunity costs. The net effect depends both on recruitment efficiency and on the ease with which insects can find work sites on their own. This study examined both of these factors for colony emigration by the ant *Temnothorax curvispinosus*. Emigrations were organized by a corps of active ants who transported the rest of the colony. These active ants either found new sites independently or followed tandem runs led by successful scouts. Although most tandem runs broke apart before reaching their target, even lost followers found the new site faster than did unguided searchers. When the new site was near the old nest, tandem runs were rare and summoned only a small proportion of the transporter corps. When the new site was instead distant and inconspicuous, tandem runs were common and brought roughly one third of the transporters. This pattern likely results from the quorum rule used by individual scouts to decide when to switch from tandem runs to transports. By monitoring how many nestmates have already found the nest, the ants ensure that the costs of recruitment are born only when necessary.

Keywords Recruitment · Communication ·
Nest site selection · Quorum-sensing

Introduction

Recruitment in the social insects is defined as communication that summons nestmates to a place where work needs

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to be done (Wilson 1971). It occurs in all major eusocial taxa and takes a great diversity of forms, including nonspecific stimulation of search (Richter 2000; Dornhaus and Chittka 2004a; Nieh 2004), direct leadership of single nestmates (Hölldobler et al. 1974; Richardson et al. 2007), mass recruitment by pheromone trails (Hölldobler and Wilson 1990; Pasteels and Bordereau 1998; Nieh 2004), and the symbolic representation of target distance and direction (Dyer 2002; Nieh 2004). The evolution of recruitment has presumably been driven by the benefits of quickly concentrating a workforce at a single location. This can improve a colony's competitive ability at rich food sources (Hölldobler 1981; Seeley 1995), marshal colony defenses against predators or competitors (Hölldobler and Wilson 1978; Detrain and Pasteels 1992), and allow an entire colony to emigrate cohesively to a distant nest site (Möglich and Hölldobler 1975; Pratt et al. 2002; Seeley et al. 2006). Moreover, recruitment is central to a colony's ability to choose the best food source or nest site, through its nonlinear amplification of differences in the attractiveness of competing options (Seeley 1995; Nicolis et al. 2003; Sumpter and Beekman 2003; Visscher 2007).

Despite these benefits, it is not always obvious how or even whether recruitment enhances the fitness of colonies that use it. It imposes both energetic and opportunity costs because discoverers of a resource must delay exploiting it to recruit to it and because some workers must forgo independent search to wait for recruitment. The balance of costs and benefits will depend partly on the efficiency of recruitment relative to independent search, which has been measured for only a few systems (Wilson 1962; Deneubourg et al. 1983; Seeley 1985; Seeley and Visscher 1988), and partly on the spatial and temporal distribution of task needs (Johnson et al. 1987; Jaffe and Deneubourg 1992; Crist and Haefner 1994; Anderson 2001; Dechaume-Moncharmont et al. 2005; Dornhaus et al. 2006). In foraging, for example, recruitment is expected to be valuable when food sources

are clumped in distribution or strongly defended but potentially detrimental when food sources are homogeneously dispersed and easy for lone searchers to find and exploit (Anderson 2001; Dechaume-Moncharmont et al. 2005; Dornhaus et al. 2006). Variation in these factors may partly explain the wide differences among species in their reliance on recruitment. Even for a single species, however, the value of recruitment may vary with time and place (Sherman and Visscher 2002; Dornhaus and Chittka 2004b). For this reason, colonies can benefit from decision rules that lead them to recruit only in appropriate circumstances (Schatz et al. 1997; Mailleux et al. 2003).

This study examined colony emigration by the ant *Temnothorax curvispinosus*, both to measure the effectiveness of recruitment and to test whether a colony's reliance on it depends on the spatial distribution of targets. These ants live in fragile preformed cavities such as hollow nuts or twigs and likely need to move often. In the laboratory, colonies thrive in artificial nests and will emigrate in arenas where the number, location, and accessibility of potential new homes can be controlled. In addition, all colony members can be uniquely identified with paint marks, allowing detailed tracking of individual behavior, including the outcome of all recruitment events. These methods have shown how emigrations are organized in *T. curvispinosus* and related species (Möglich 1978; Franks et al. 2002; Pratt et al. 2002; Pratt 2005a). A subset of active workers search for new homes and use two distinct techniques to recruit nestmates to promising finds. Early in the emigration, they use tandem runs to lead fellow active ants, one at a time, to the new site (Möglich 1978; Richardson et al. 2007). This method is slow, but it allows followers to learn the route so that they can afterward recruit on their own. Later in the emigration, recruiters abandon tandem runs for social transports, in which nestmates are simply carried from the old nest. Although carried ants cannot learn the route, this speedier method is better suited to efficient movement of many ants. The switch in recruitment behavior is governed by a quorum rule. Recruiters monitor the density of ants at the new site through their rate of encounter with one another (Pratt 2005b). Once they sense that the density has surpassed a threshold, they begin the transport phase (Pratt et al. 2002). In short, the early tandem phase summons a corps of transporters who move the passive majority of the colony in the transport phase.

Tandem runs play a prominent role in this scheme, but how effective are they at bringing scouts to a site? An answer to this question must account for the roughly three quarters of tandem pairs that break up before reaching their target (Pratt 2005a; Pratt et al. 2005). These apparent failures might contribute significantly to recruitment, if the orphaned followers enjoy a higher probability of finding the site during a subsequent independent search, compared to scouts that have not been led. Therefore, to estimate tandem effectiveness, I compared the per capita discovery rate of tandem followers with that of ants searching independently. The prediction was that tandem followers would enjoy higher discovery rates, even when they lost contact with their leader before arriving at the new site.

If tandem runs improve discovery rates, their value to the colony may still depend on the distance and conspicuousness of recruitment targets. If it is relatively easy for independent scouts to find sites on their own, then a sufficient transport corps might assemble quickly without recruitment. In these circumstances, scouts would do better to avoid time-consuming and unnecessary tandem runs in favor of other tasks, such as defending a site they have found, searching for a better one, or starting to transport nestmates. The ants' quorum rule could bring this about, by cutting off tandem runs quickly when independent discoveries are common. To test this hypothesis, I measured the number and role of tandem runs when colonies emigrated either to a distant, partially hidden site in a large arena or to a nearby, exposed site in a small arena. The prediction was that tandem runs would be significantly less common in the short emigration and that they would contribute less to summoning the transport corps.

Materials and methods

Experimental colonies

Colonies of *T. curvispinosus* were collected in March and August 2003 in Princeton, NJ (40° 19′ 45″ N, 74° 39′ 55″ W) from acorn and hickory nut nests. In the laboratory, they were housed in nests made from a slat of balsa wood sandwiched between two microscope slides. A nest cavity was cut through the middle of the slat, and a small entrance hole was drilled through the roof slide. Nests were kept in covered Petri dishes (15 cm diameter) with Fluon-lined walls to prevent the ants from escaping. Ants were fed ad libitum with water, fruit flies, and an agar-based diet (Bhatkar and Whitcomb 1970). Colonies had one to five queens, 80 to 190 workers, and 110 to 180 brood items. Workers were marked with individually specific patterns of four paint drops on the head, alitrunk, and gaster. Experiments were conducted from March to August 2004.

Emigrations

Emigrations were observed under two treatments that differed in the ease with which scouts could find the new nest. In each treatment, emigration was induced by removing the roof of the colony's nest and providing an intact new nest nearby. The "long" treatment used a large

arena (4,500cm^2) in which the nests were 65cm apart (Fig. 1a). Discovery was hindered by surrounding the new nest with a circular plastic wall, 2.5cm tall and 14cm in diameter. A Fluon coating on both sides of the wall prevented the ants from climbing over it; they could enter and leave the enclosure only through a single small entrance (2mm diameter) at the base of the wall. Wooden blocks were placed around the arena to provide visual landmarks for navigation. The "short" treatment was carried out in a small arena (400cm^2) where the old and new nests were only 11cm apart and the new nest was not concealed behind a wall (Fig. 1b). The small arena was placed inside the large arena so that ants could see the same visual landmarks as in the "long" treatment. In both treatments, colonies were placed in the arena immediately before the start of the emigration and returned to their nest boxes once the emigration was complete. A digital video camera (Sony TRV30) recorded all entries, exits, and transports at the new
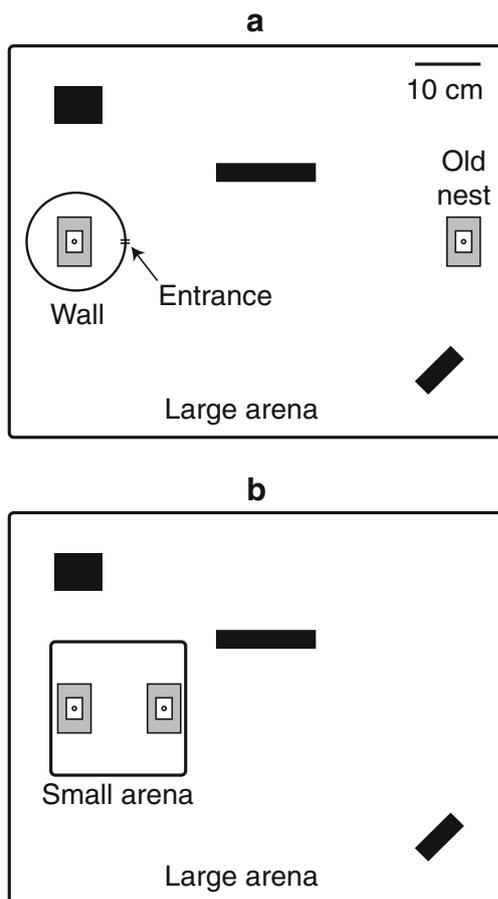

Fig. 1 Layout of emigration arenas. **a** In the long treatment, the new nest was hidden within a circular enclosure accessible by a single small entrance hole. *Black rectangles* show the locations of visual landmarks. **b** In the short treatment, ants moved in a smaller arena to an unconcealed nest. The small arena was placed inside the large one to give similar visual cues in each treatment

nest. In addition, an observer watched the arena and recorded the timing and participants of all tandem runs. If a tandem run broke up before reaching the new nest, the approximate location of the breakup was noted.

Each of three colonies was tested first in the long treatment and 8 or 9days later in the short treatment. These data were supplemented with an additional six emigrations in each treatment, observed as part of an unrelated experiment (Pratt and Sumpter 2006). The additional short treatments used the same three colonies as before, but the long ones used three other colonies. Each colony emigrated twice, once to a high-quality nest (identical to those used in the emigrations described above) and once to a lower-quality nest (its entrance diameter was three times greater). Methods for the long treatments were identical to those described above, but the short treatments differed as follows: (1) nests were separated by 15cm, (2) the small arena was not placed inside the large arena, hence the landmarks were not available, (3) colonies were placed in the arena the day before the emigration, and (4) the arena was capped with a glass lid. When analyzed separately, these additional emigrations yielded the same results as the combined data for all emigrations, hence only the combined results are presented below.

Measurement of nest discovery rate

The per capita discovery rate of ants searching independently was compared with that of ants that had followed tandem runs. Rates were estimated by using the survival analysis library in the statistical package R to fit an exponential distribution to the search intervals of individual ants. For a tandem follower this interval started when the ant began following and ended when she first entered the new nest. Because most tandem followers lost contact with their leader before finding the new nest, the interval included time spent searching alone after tandem breakup. For independent searchers, the search interval began at the start of the emigration (that is, the removal of the old nest's roof) and ended either when the ant entered the new site or when she began to follow a tandem run. During this interval, ants typically alternated between active search and resting in the old nest. To take this into account, the observed intervals were multiplied by the estimated proportion of time the ants spent outside the old nest. This estimate was derived from a single long emigration in which a video camera at the old nest recorded all entries and exits there. From these data were measured the durations of searches in the arena and stays at the old nest by active ants. Measurements were confined to a 30-min period near the start of the emigration. The rate D at which ants departed the old nest was estimated by survival analysis of rest durations. The rate R at which ants returned

to the old nest was similarly estimated from search durations. The proportion of time spent by nonfollowers outside the old nest was estimated as $D/(R + D) = 0.19/(0.07 + 0.19) = 0.73$. Further details on this emigration are reported in Pratt (2005a).

Ants were counted as independent searchers only if they were active emigration participants, defined as workers that transported at least one nest mate, led or followed at least one tandem run, or independently discovered the new site. If an independent search ended with the ant becoming a tandem follower, the interval was treated as censored data in the survival analysis. Also censored were searches by active ants that had not found the new nest before the end of videotaping. This happened only in one very slow long emigration. An effect of tandem running on discovery rate was tested by using the *survreg* function in R to regress search durations on search type (following or independent).

Assessment of tandem run contribution

The video recordings were used to make three measures of the contribution of tandem runs to each emigration. First, all transporters were classified according to whether they discovered the nest independently (nonfollowers) or only after following a tandem run (followers). Ants were considered followers even if they lost contact with the tandem leader before reaching the new nest. Second, the total number of transports completed by each class of discoverer was counted. Third, the number of ants in each class that had found the nest by the time of the first transport was counted. This provided a measure of the relative contribution of followers and nonfollowers to quorum attainment. For each of these metrics, a Wilcoxon test was used to identify differences between treatments.

Results

Enhanced discovery rate by tandem run followers

In the long treatment, ants that followed tandem runs found the new nest over five times more rapidly than ants that did not (Fig. 2a). This was despite the fact that 82 of the 117 followers (70%) lost contact with their tandem leader before reaching the new nest. Even these lost followers found the new nest three times more rapidly than nonfollowers, a statistically significant difference (Fig. 2a). For 27 incomplete tandem runs, the approximate place at which they broke apart was noted: Three did so near the old nest, 18 made it most of the way across the arena but ended outside the wall, and only six entered the wall. Even the 21 pairs that broke up outside the wall found the new nest significantly faster ($0.35 \pm 0.09h^{-1}$) than did nonfollowers

in the same emigrations ($0.15 \pm 0.03h^{-1}$) ($\chi_1^2 = 8.1$, $n = 92$, $p < 0.01$).

Results for the short treatment were similar when all followers were considered, but the discovery rate of lost followers did not significantly exceed that of nonfollowers (Fig. 2b). In addition, all discovery rates were higher in the small arenas, and only 13 of the 30 tandem followers (43%) got lost. The endpoint for seven of the incomplete tandem
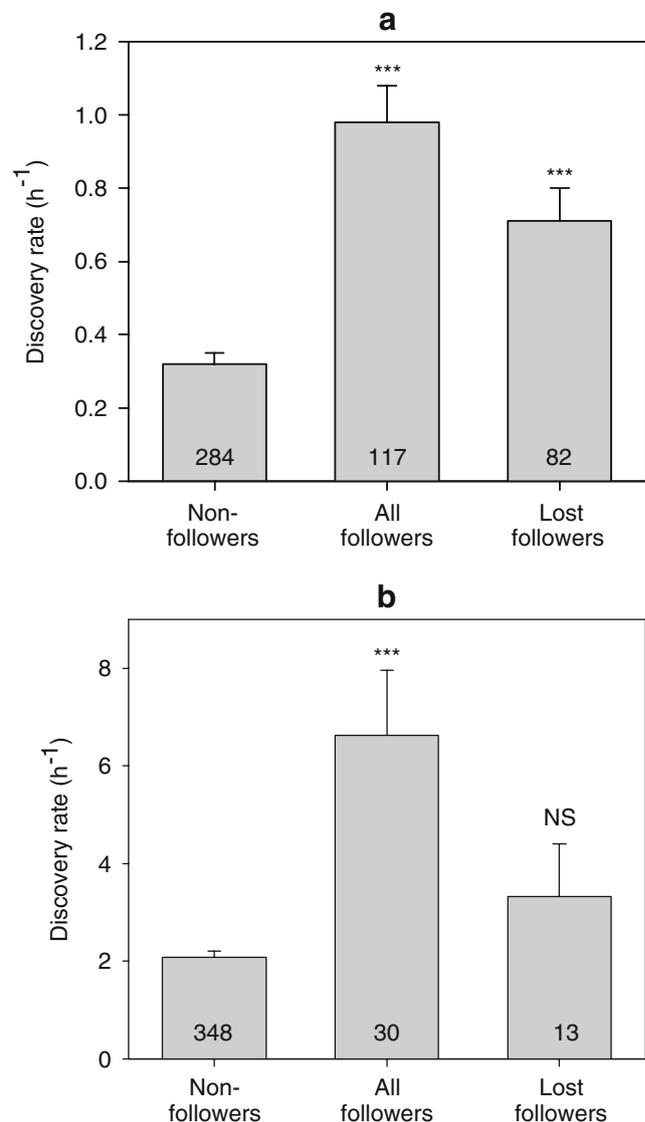

Fig. 2 Comparison of per capita nest discovery rates for ants that followed tandem runs and ants that did not. The discovery rate of followers was measured twice: once using all followers and once using only those that lost contact with their tandem leader. **a** In the long treatment, the rate for nonfollowers was significantly exceeded by the rates for all followers ($\chi_1^2 = 74.4$, $n=401$, $p<0.0001$) and for lost followers ($\chi_1^2 = 29.9$, $n=366$, $p<0.0001$). **b** In the short treatment, the rate for nonfollowers was significantly exceeded by the rate for all followers ($\chi_1^2 = 27.0$, $n=378$, $p<0.0001$) but not by the rate for lost followers ($\chi_1^2 = 2.4$, $n=361$, $p=0.12$). *Numbers on bars give sample sizes*

runs was noted: All broke up on or within a few centimeters of the new nest.

Tandem run contribution and emigration distance

Long emigrations had significantly more tandem runs than short emigrations (Fig. 3a). Moreover, tandem recruitment made a stronger contribution to the transport effort in the long treatment, where $36 \pm 20\%$ of transporters found the new nest after following a tandem run, compared to only $7 \pm 7\%$ in short emigrations (Wilcoxon test: $p < 0.01$, $n = 18$; Fig. 3b). Tandem followers were responsible for a correspondingly higher proportion of total transport effort in the long treatment ($35 \pm 20\%$) than in the short one ($8 \pm 8\%$; Wilcoxon test: $p < 0.01$, $n = 18$; Fig. 3c). Finally, followers made up a larger proportion of the ants potentially contributing to quorum attainment in the long treatment ($31 \pm 25\%$) than in the short one ($6 \pm 6\%$; Wilcoxon test: $p < 0.01$, $n = 18$; Fig. 3d).

Two of the long emigrations lasted over 8h and were not watched until completion. If the relative number of followers increases over the course of an emigration, then the observed treatment effects on numbers of transporters and transports might really be artifacts of missing data. To test this hypothesis, the analysis was repeated without these emigrations The proportion of followers remained significantly higher in the long treatment (Wilcoxon test: $p < 0.01$, $n = 16$), as did the proportion of transports by followers (Wilcoxon test: $p < 0.05$, $n = 16$). Thus, the hypothesis that treatment differences are due to missing data can be rejected.

Discussion

Tandem runs—even those that appeared to fail—significantly increased the rate at which scouts of *T. curvispinosus* found a new nest site. The value of this enhancement to the colony's emigration, however, depended very much on the search context. In the short treatment, incomplete tandem runs did not significantly improve discovery rates over independent search, perhaps because partial recruitment could do little to increase the already very high discovery rates in the small arenas. More importantly, tandem
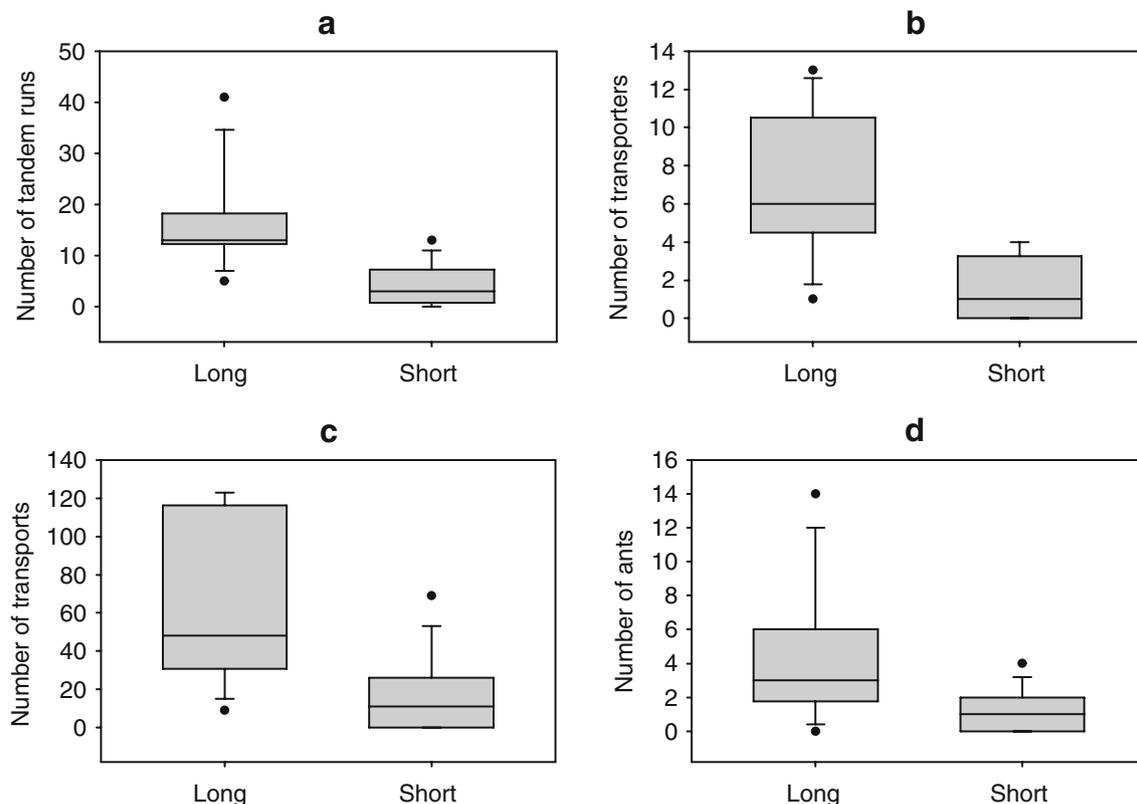

Fig. 3 Comparison of tandem run contribution to long and short emigrations. **a** The total number of tandem run followers was significantly greater in the long treatment (Wilcoxon test: $W=75.5$, $n=18$, $p<0.01$), as were **b** the number of transporters recruited in tandem runs (Wilcoxon test: $W=73.0$, $n=18$, $p<0.01$), **c** the number of transports completed by ants recruited in tandem runs (Wilcoxon test: $W=69.0$, $n=18$, $p<0.05$), and **d** the number of ants contributing to the quorum that were recruited in tandem runs (Wilcoxon test: $W=65.0$, $n=18$, $p<0.05$). The *ends of each box* mark the upper and lower quartiles, the *horizontal line* shows the median, *brackets* show the 10th and 90th percentiles, and *points* show outliers

recruitment was responsible for only about 15% of quorum attainment and transport effort in the short treatment. In the long treatment, where sites were more distant and obscure, this proportion rose to roughly one third.

There are two ways that tandem runs could enhance discovery rate, even without bringing followers all the way to the new nest. First, they might directly improve search efficiency by bringing scouts near the new site, where they find it more rapidly than would unguided ants. Second, tandem runs might simply increase search effort by rousing ants to leave the old nest. The current results support a direct effect on search efficiency because they show that following a tandem run significantly boosts discovery rate, even when independent search durations are corrected to omit time spent inside the old nest. That is, the difference in discovery rates cannot be ascribed to tandem followers spending more time searching than do nonfollowers. Of course, this does not rule out a simultaneous effect on search effort, if tandem recruitment increases the likelihood of an ant leaving the old nest. Another factor deserving further research is the potential role of pheromonal signals deposited near the new nest or along the route to it. These ants do not appear to use chemical recruitment trails, but there is some evidence for individual-specific orientation trails and substrate marking in other *Temnothorax* species (Maschwitz et al. 1986; Mallon and Franks 2000). Such cues might contribute to a lost follower's ability to locate the new site.

Although incomplete tandem runs are clearly effective, the rate of tandem breakup still seems remarkably high. This could be an artifact of the laboratory environment—a largely empty plastic tray may not offer enough of the visual cues that *Temnothorax* ants rely on for navigation (Aron et al. 1988; McLeman et al. 2002). Moreover, ants were placed in the arenas at most 1day before emigrating and so had little time to learn those cues that were available. As a result, tandem leaders may take especially long, winding paths, increasing the likelihood that their followers will lose contact before arriving at the target. It may be that tandem runs break up less in nature, where navigation cues are better. On the other hand, tandem recruitment may be an inherently noisy process. If so, it shares this feature with other recruitment systems for which efficiency has been directly measured. Honey bee recruits, for example, make four or more unsuccessful search flights, each preceded by dance following, before arriving at the advertised food source (Seeley 1985). Ants following pheromone trails also frequently become lost before reaching the recruitment target, at least for trails that have not been reinforced by a large number of ants (Wilson 1962; Deneubourg et al. 1983; Robson and Traniello 1998).

This noisiness is not necessarily a limitation because recruitment serves not only to move workers quickly but also to bring them to the best targets. Thus, while honey bee dance followers take longer than unguided scouts to find a feeding site, they end up retrieving more food, on average, because waggle dances are preferentially directed at high-quality sites (Seeley and Visscher 1988). Ant foragers that lose a pheromone trail help the colony to discover new resources and to avoid becoming fixated on the first source they encounter, even when better ones are available (Detrain and Deneubourg 2006). For house-hunting *Temnothorax*, the need for rapid emigration must compete with the goal of thoroughly exploring all possible options (Franks et al. 2003; Pratt and Sumpter 2006). Recruitment that is too speedy and efficient may cause the ants to miss out on an excellent site if they happen to find a mediocre one first.

Regardless of its efficiency, recruitment is potentially costly when performed unnecessarily. If independent discoveries can rapidly assemble a transporter force, ants would do well to skip tandem runs in favor of more rewarding tasks. The present study shows that they can regulate recruitment in this way. This ability helps to explain why tandem runs, despite their apparent importance to the organization of colony emigration, are often quite rare in laboratory observations. In earlier studies, where nest sites were generally nearby and easy to find, fewer than 10% of transporters found the new nest after following a tandem run; most instead discovered it independently (Mallon et al. 2001; Pratt et al. 2002; Pratt et al. 2005). Although detailed observations of emigrations in nature have not been reported, it seems likely that ants face travel distances and spatial complexity at least as great as in the long treatment of this study. If so, colonies may often rely heavily on tandem recruitment to sites that they would otherwise find with difficulty.

The ants' adjustment of tandem run prevalence most likely results from their quorum rule. By conditioning tandem running on the population at the target site, ants ensure that they abandon it quickly if independent discoveries are common. On the other hand, they will continue tandem recruitment as long as necessary to a site that is encountered by a few unguided ants. Analogous examples of recruitment regulation are known in social insects but generally involve direct assessment of the properties of the recruitment target. Foraging ants, for instance, cease reinforcing an odor trail to food once saturation of the source by exploiters stops new arrivals from being rewarded (Hölldobler and Wilson 1990), and many predatory ants recruit to prey only if solitary retrieval fails (Schatz et al. 1997). *Temnothorax* workers, in contrast, monitor a property of the colony itself—the number of nestmates informed of the site and thus able to serve as transporters. An advantage of this cue is that it can integrate two very different influences on the usefulness of recruit-

ment. One, addressed in this study, is the location and conspicuousness of the site itself. The other is the amount of effort that the colony puts into search. If relatively few ants are looking for new nests, then independent discovery rates may be low, and tandem recruitment may be more important in summoning transporters. If the colony invests heavily in search, then more independent discovers will quickly find each site, even those that are relatively distant or obscure. This might be the case, for example, when a crisis at the old nest places a high premium on speedy emigration and so causes ants to deploy many searchers (Pratt and Sumpter 2006).

Analogous threshold rules influence the balance of scouting and recruitment in other social insects. A honey bee forager, for example, recruits to a rich food source only if she experiences less than a threshold delay in finding a food storer to receive her nectar load (Seeley 1995). Among trail-following ants, a forager's probability of joining a trail appears to be a threshold function of its strength, determined by the number of workers who have already reinforced it (Beckers et al. 1990; Sumpter and Beekman 2003). More generally, many social animals employ quorum-like rules under which an individual joins in a behavior only if a minimum number of other group members are already participating (Sumpter and Pratt 2008). Previous theoretical and empirical studies have shown that this kind of rule can help a group make more accurate consensus decisions (Franks et al. 2003; Passino and Seeley 2006; Pratt and Sumpter 2006; Sumpter and Pratt 2008). The current results show how it can also contribute to adaptive regulation of a colony's investment in costly recruitment.

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