

Research article

Behavioral mechanisms of collective nest-site choice by the ant *Temnothorax curvispinosus*

S.C. Pratt

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, U.S.A., e-mail: spratt@princeton.edu

Received 11 February 2005; revised 10 May 2005; accepted 20 May 2005.

Abstract. This paper examines the individual behavior underlying collective choice among nest sites by the ant *Temnothorax* (formerly *Leptothorax*) *curvispinosus*. Colonies can actively compare options, rejecting a mediocre site when it is paired with a good one, but accepting the same mediocre design if it is instead paired with a worse site. This ability emerges from the behavior of an active minority of workers who organize emigrations. When one of these finds a promising site, she recruits nest mates to it, but only after a delay that varies inversely with site quality. Ants first recruit fellow active ants via slow tandem runs, but eventually switch to speedier transports of the colony's passive majority. Later transports grow faster still, as ants improve their speed with experience. An ant's choice of recruitment type is governed by a quorum rule, such that her likelihood of starting to transport increases with the population of the new site. The size of the quorum depends on experience, with ants demanding a larger population to launch immediately into transport than they do to switch to transport after first leading a few tandem runs. Perception of quorum attainment requires direct contact between ants. The ants' behavior qualitatively matches that of *T. albipennis*, where models have shown that decentralized choice of the best site depends on quality-dependent recruitment delays, amplified by a quorum rule for initiating transport. Parameter estimates for an agent-based model show significant quantitative differences between the species, and suggest that *T. albipennis* may place relatively greater emphasis on emigration speed.

Keywords: Collective decision-making, *Leptothorax*, *Temnothorax curvispinosus*, quorum sensing, nest-site selection.

Introduction

Insect societies owe much of their ecological success to a highly distributed organization of information and labor

(Camazine et al., 2001; Hirsh and Gordon, 2001; Seeley, 1995; Theraulaz et al., 2003). Without any central control, colonies can integrate the piecemeal actions of their many members into coordinated, robust, and efficient group behavior. Thus, an emigrating colony of the ant *Temnothorax* (formerly *Leptothorax*) *albipennis* can collectively choose the best of several available nest sites, even when few of the individual ants organizing the emigration have visited all sites (Mallon et al., 2001). Understanding such a process entails two steps: first, identification of the decision rules, communication signals, and information sources guiding the behavior and interactions of individual insects; second, the application of mathematical models and computer simulations to test the adequacy of these individual characteristics to generate observed collective phenomena. Moving from the first to the second step requires a detailed quantitative characterization of individual behavior, information that is currently available for very few systems (for example, Mailleux et al., 2003; Seeley, 1995; Seeley and Visscher, 2004). The comparative study of collective cognition by social insects would benefit from intensive understanding of a wider array of species.

Colony emigration in the species-rich genus *Temnothorax* is a particularly promising subject for this work. These ants form small colonies of no more than a few hundred workers, and typically nest in pre-formed cavities, such as hollow twigs, seed husks, and rock crevices. The vulnerability of these sites likely necessitates frequent emigrations (Möglich, 1978). Extensive study of the old world species *T. albipennis* has shown in detail how these emigrations are organized (Dornhaus et al., 2004; Franks et al., 2002, 2003a; Langridge et al., 2004; Mallon et al., 2001; Pratt, 2005; Pratt et al., 2002, 2005). About one-third of the colony's workers serve as recruiters, searching for new sites and bringing nest mates to promising finds (Pratt et al., 2002). They first recruit only fellow active ants via tandem runs, in which a single ant is slowly led from the old nest to the new (Möglich, 1978). Later, they transport the passive majority of the colony

(including queens and brood), by picking them up one at a time and carrying them to the new site. During the transport phase, recruiters occasionally lead “reverse” tandem runs from the new nest back to the old. Tandem runs are significantly slower than transports, but they may better allow followers to learn the route to the new nest, so that they can later recruit on their own.

When given a choice, colonies show clear preferences for certain nest designs over others, distinguished by cavity size, entrance diameter, and light level (Franks et al., 2003b; Mallon and Franks, 2000; Mallon et al., 2001). These preferences do not result from mere satisficing, i.e. taking without prejudice the first candidate site that exceeds a threshold quality (Todd and Gigerenzer, 2000). Instead, they reflect active comparison among available options, such that a given site will be clearly rejected when paired with a superior design, but just as strongly preferred if paired instead with a worse design (Mallon et al., 2001).

These comparisons partly emerge from the ability of active scouts to confine their recruitment to the better of two sites that they have visited (Mallon et al., 2001). The importance of this ability is limited, however, because scouts do not typically visit both sites in the course of an emigration. A collective comparison instead emerges from competition between independent recruitment efforts at each site. Scouts follow two key decision rules that increase the chance of the better site winning this competition. First, they start recruitment to a site only after a latency inversely proportional to site quality (Mallon et al., 2001). This causes stronger positive feedback on population growth at better sites. Second, a scout’s probability of switching from tandem runs to transports increases with the number of nest mates already present at the new site (Pratt et al., 2002). The switch is apparently mediated by the ant’s rate of tactile encounters with nest mates at the site, rather than by indirect, pheromonal cues (Pratt, 2005). The quorum rule amplifies the quality-dependent difference in recruitment strength, because faster population growth at better nests means that they experience accelerated recruitment earlier. Ideally, this allows the best site to absorb all of the colony’s passive members before lesser competitors have made the switch. These rules are sufficient to account for the decision-making abilities of *T. albipennis*, according to an agent-based model that incorporates a detailed, quantitative description of individual behavior (Pratt et al., 2005).

In this paper I investigate nest-site selection by the New World species *T. curvispinosus*. The behavior of these ants shows at least a superficial similarity to that of *T. albipennis*, with early tandem runs giving way to a transport phase punctuated by occasional “reverse” tandem runs (Möglich, 1978). *T. curvispinosus* colonies can also discriminate among nest designs, preferring those with larger cavity volume, smaller entrances, and higher cavity ceilings (Pratt and Pierce, 2001). Here I show that these preferences are based on active comparison among available alternatives, rather than satisficing. I then use videotaped emigrations of individually marked ants to show that workers organize emigrations with similar rules to those described in *T. albipennis*. Finally, I precisely

characterize these rules by applying to *T. curvispinosus* the agent-based model originally developed for *T. albipennis*. Comparison of the model’s parameter values reveals significant quantitative differences in the qualitatively similar decision algorithms used by these species.

Methods

Preference tests

Colonies of *Temnothorax curvispinosus* were tested for preferences among three nest types. Each type consisted of a balsa wood slat (2.4 mm thick) sandwiched between two glass microscope slides (50 × 76 mm). A nest cavity was cut through the middle of the slat, and a round entrance hole drilled through the center of the roof slide. Nest type A had a large rectangular cavity (25 × 33 mm) and a small entrance hole (1.6 mm diameter). Nest type B had an identical cavity, but a larger entrance (4.8 mm diameter). Nest type C had both a round cavity of smaller size (17 mm diameter) and a still larger entrance hole (9.5 mm diameter). On the basis of earlier tests (Pratt and Pierce, 2001), the sequence A to C was expected to represent worsening nest quality to the ants.

Separate tests were made for each of the three possible pairings of nest types: A vs. B, B vs. C, and A vs. C. For each pairing, preference was assayed by offering each of 12 colonies a choice between the two types and noting which nest it moved into. The same 12 colonies were used for all three pairings, introducing the possibility that a colony’s experience with one pairing could influence its preference in later tests. To avoid any resulting bias, colonies received the tests in different orders, such that the six possible orderings of the three pairings were equally represented.

In each test emigration, a colony, housed in an intact nest, was placed against one wall of a 20 × 20 cm clear plastic assay dish. Alternative new nests were placed at opposite corners. To control for side bias, each pairing was offered an equal number of times in each left/right configuration. Six test sessions were run, each consisting of six emigrations carried out simultaneously. In a given session, the lidded dishes were stacked on top of one another and separated by a paper towel, to mask visual cues offered by the behavior of neighboring colonies. The stack was centered beneath a fluorescent ceiling light, and its sides shielded with white fiberglass boards to prevent external light gradients or other visual cues from biasing the ants. Emigrations were induced by removing the roof of the old nest. The proportion of a colony’s members in the lower-lettered site was noted on the following day. For example, in tests of design A vs. design B, I noted the proportion in site A. If colonies have no preference between A and B, then the mean proportion moving to A should not be different from one half. A Wilcoxon signed rank test was used to detect any significant difference from this expectation. The same approach was used for the other two pairings. Testing proportions, rather than simply scoring each choice as one site or the other, allowed for analysis of a minority of colonies that split between the sites. Colony populations ranged from 44 to 304 workers, with 1 to 6 queens and ample brood. These colonies, and all others used in this study, were collected in Princeton, New Jersey.

Behavior of individual ants

Three colonies of individually marked ants were induced to move successively to high and mediocre quality nests, as determined by the preference tests described above. Ants were marked with four drops of paint on the head, thorax, and gaster. Emigrations were observed in a large tray (75 × 60 × 7 cm) the walls of which were coated with Fluon to prevent the ants’ escape. Balsa blocks were strewn about the cavity to serve as visual landmarks for orientation. An inhabited nest was placed against one wall of the tray and a single empty nest near the opposite wall, 60

cm away. The new nest was surrounded by a circular, Fluon-coated, polystyrene wall, 2.5 cm high and 14 cm in diameter, with a single small entrance, 2 mm in diameter, drilled through its side. By reducing the rate at which scouts discovered the nest, this wall increased the number of recruitment decisions observed at low nest populations, and thus enhanced detection of population effects on recruitment choice. Digital video cameras recorded the ants' activity at both old and new nests. Three colonies were observed, with populations of 80 to 120 workers, 1 to 5 queens, and 130 to 150 brood items. Each colony moved first to the better nest, and three to five days later to the mediocre nest. Detailed records of the behavior of each ant were compiled from the videotapes and used to characterize the ants' behavior, as described below.

Division of labor and recruitment type

Division of labor was measured by counting each worker's recruitment acts. To determine whether an ant's recruitment effort was associated with the way that she arrived at the new nest, I classified each worker into one of three arrival types: 1) Discoverers walked into the nest without first having followed a tandem run for at least one minute; 2) Transportees were carried into the nest; 3) Followers were led in a tandem run toward the new nest for at least one minute before walking into the new nest. Ants were scored as followers even if they lost contact with their tandem leader before entering the new nest, because these incomplete tandems markedly increase a recruit's probability of finding the nest (personal observations). To test for effects of arrival type and nest quality on recruitment effort, the data were fit to a generalized linear model (McCullagh and Nelder, 1989).

In *T. albipennis*, a minority of transportees later become recruiters, but these transports are disproportionately likely to begin in the arena, rather than inside the old nest (Pratt et al., 2002). To determine whether a similar pattern holds in *T. curvispinosus*, I calculated the proportion of recruiting transportees picked up in the arena and compared this to the corresponding value for an identical number of randomly chosen non-recruiting transportees.

Recruitment speed

The speed of tandem runs and transports was compared by measuring the duration of each recruitment trip, from an ant's leaving the new nest to her return with a recruit. In *T. albipennis*, these trips grow briefer with successive recruitment acts, probably because the ants improve their ability to navigate the route to the old nest (Pratt et al., 2005). To account for any similar effect here, trip durations were plotted as a function of their position n in the ant's sequence of recruitments, and these data fitted to the following function:

$$D = b - a \left(\frac{n - 1}{k + n - 1} \right)$$

where D is the expected round-trip duration, b is the duration at the first recruitment and k determines how fast the duration approaches its asymptotic value $b - a$. This function was fit either with common parameter values for both recruitment types, or separate ones for each, and the goodness of fit compared to test for a significant effect of recruitment type on journey duration.

Recruitment initiation rate

To determine whether ants initiate recruitment more rapidly at better nests, I measured the latency between each active ant's arrival at the new nest, and her first departure from it to recruit. Active ants included all those that transported a nest mate, led or followed a tandem run, or independently discovered the new nest site. Some active ants had not begun to recruit by the emigration's end. To account for these, the data were analyzed by survival analysis, with non-recruiters scored as censored data and their latencies terminated at the time when 90% of total transports had been completed. Latencies were fit to an exponential distribution and tested for an effect of nest quality on the exponential parameter (i.e., the rate at which an ant begins to recruit).

All three colonies moved first to the better nest, and then to the mediocre one, introducing a potentially confounding effect of test order.

In particular, ants might start recruitment more quickly in the second emigration, purely as a result of experience. In *T. albipennis*, colonies emigrate faster when induced to move within seven days of a previous emigration, an effect which plausibly involves changes in recruitment initiation rate (Langridge et al., 2004). Such an effect may also be present in *T. curvispinosus*, but two factors would minimize its potential significance. First, the learning effect in *T. albipennis* soon saturates, with third and later emigrations showing no significant gain in speed. Each colony in the present study had made a pilot emigration in the same arena, no more than two to six days before the first experimental emigration. Assuming a comparable saturation effect in both species, no acceleration should have been detectable between the two experimental emigrations. Second, even if a learning effect is present, it will render the statistical test more conservative, by speeding emigrations to mediocre nests and thus diluting any tendency for faster recruitment initiation at good nests.

Quorum rule

For each independent recruitment decision, I noted the recruitment type chosen and the mean population of the new nest during the ant's immediately preceding visit there. Independent decisions were those up to and including each ant's first transport, because observations on *T. albipennis* show that ants cease monitoring nest population once they start transporting (Pratt, 2005). Recruitment decisions were scored as either 0 (tandem run) or 1 (transport), and their dependence on population fitted with a Hill function, a mathematically simple and general way to represent switch-like responses:

$$S = \frac{P^k}{T^k + P^k}$$

S is the probability of switching to transport, P is the mean nest population, and k determines the nonlinearity of the response, with higher k yielding a more step-like function. T is the mean population at which S equals 0.5, and may be taken as the size of the quorum needed for ants to switch to transport. This function was fit either with common parameter values for all recruitment decisions, or with one set of values for each ant's first decision and a separate set for all later decisions. The goodness of fit of the two versions was then compared to determine whether ants use an especially high or low quorum on their first decision. A similar approach tested for an effect of nest quality.

A separate experiment directly tested for an effect of site population on recruitment type. The design followed closely an experiment previously carried out on *T. albipennis* (Pratt, 2005). Colonies were induced to emigrate to a special two-chambered nest. The lower chamber was freely accessible to the ants and was separated by a double layer of fine mesh from a closed upper chamber. Emigrations were observed in an arena devised to allow experimental control of the number and identity of workers entering the new nest. In each experiment, one of four individually marked queenright colonies was induced to launch an emigration. Once five transports had been completed, the colony was subjected to one of three treatments: 1) No Ants: The new nest and its occupants were removed from the arena and replaced with an empty nest that had never been visited by any ant. 2) Ants/Full Contact: All ants were removed from the new nest, and then immediately returned there. 3) Ants/No Contact: All ants in the new nest were moved to the upper nest chamber, leaving the lower chamber completely empty. Six candidate focal ants who had been sequestered from the rest of the colony at the start of the emigration were then returned to the arena. These ants, but no others, were allowed to find the new nest and to begin recruitment. If the number of ants at the new site determines recruitment behavior, then the focal ants were expected to choose tandem runs when recruiting to a completely empty nest (No Ants), and transports when allowed full contact with a quorum of nest mates (Ants/Full Contact). If the number of ants is not important, then ants were expected to show similar recruitment behavior in each treatment. In the event that an influence of population was supported, the third treatment (Ants/No Contact) tested the route by which ants detect the presence of nest mates. If physical contact is required, the focal ants

were expected to choose tandem runs. If indirect cues suffice, they were expected to choose transports.

Quantitative comparison to *T. albipennis*

Data from the videotaped emigrations were used to estimate parameters of a detailed agent-based model of emigration behavior (Pratt et al., 2005). Corresponding estimates were made for twelve emigrations by colonies of *T. albipennis* using nests of similar design, although different features distinguished good from mediocre nests (Mallon et al., 2001; Pratt et al., 2005). Estimates were then tested for significant differences between the species. Parameter definitions, given below, generally follow those in (Pratt et al., 2005), where further details can be found. Some definitions have been simplified by lumping estimates for different recruitment types or emigration stages.

ActiveWorkers: proportion of workers actively scouting or recruiting during an emigration.

RecTime: mean round-trip recruitment duration, as described above. For comparative purposes, I report the expected duration of the first and fourth trips (for tandem runs), and the first and tenth trips (for transports). This roughly indicates the slowest and fastest of each recruitment type observed, because few ants led more than four tandems, and trip speeds had largely stopped improving by the tenth transport (see Results). Before analysis, the durations for *T. albipennis* were first multiplied by 0.92 to account for the slightly longer inter-nest distance used in those emigrations (65 cm).

Quorum: nest population at which a recruiter has a 50% probability of switching from tandem runs to transports; i.e., the value of T in the Hill function described above. This was calculated separately for each ant's first recruitment decision and for later recruitment decisions.

Recruit: rate at which recruiters leave the new nest to lead a tandem run or begin a bout of transports.

PauseTrans: probability that an ant interrupts a bout of transports to explore the arena.

TransInNestTime: time spent inside the new nest between recruitment trips during a bout of transports.

Reverse: probability that an ant returning to the old nest to transport leads a reverse tandem run on the way.

PropLost: proportion of initial followers of tandem runs who lose contact with their leader before entering the new nest. Followers were not scored as lost if they reached the new nest within 30 seconds of the leader's arrival. Only tandem runs to the new nest were analyzed.

PickedUp: rate at which active ants walking in the arena are picked up and transported to the new nest.

Statistical analysis

Analyses were performed with the statistical package R (Venables and Ripley, 2002). Several methods were used to detect species effects on parameter values: Wilcoxon test (ActiveWorkers); logistic regression (Reverse); regression for an exponential survival model (Recruit); multinomial model (PropLost, PickedUp); and least-squares fits to either non-linear (RecTime, Quorum) or linear (TransInNestTime, PauseTrans) models. Unless otherwise noted, summary data are reported as mean \pm standard deviation.

Results

Nest preferences

Colonies significantly preferred nest type A to nest type B (Wilcoxon signed rank test: $V = 67$, $P < 0.05$), nest type B to nest type C ($V = 71.5$, $P < 0.01$), and nest type A to nest type C ($V = 78$, $P < 0.001$) (Fig. 1). Preferences are therefore transitive, and they indicate an ability to compare

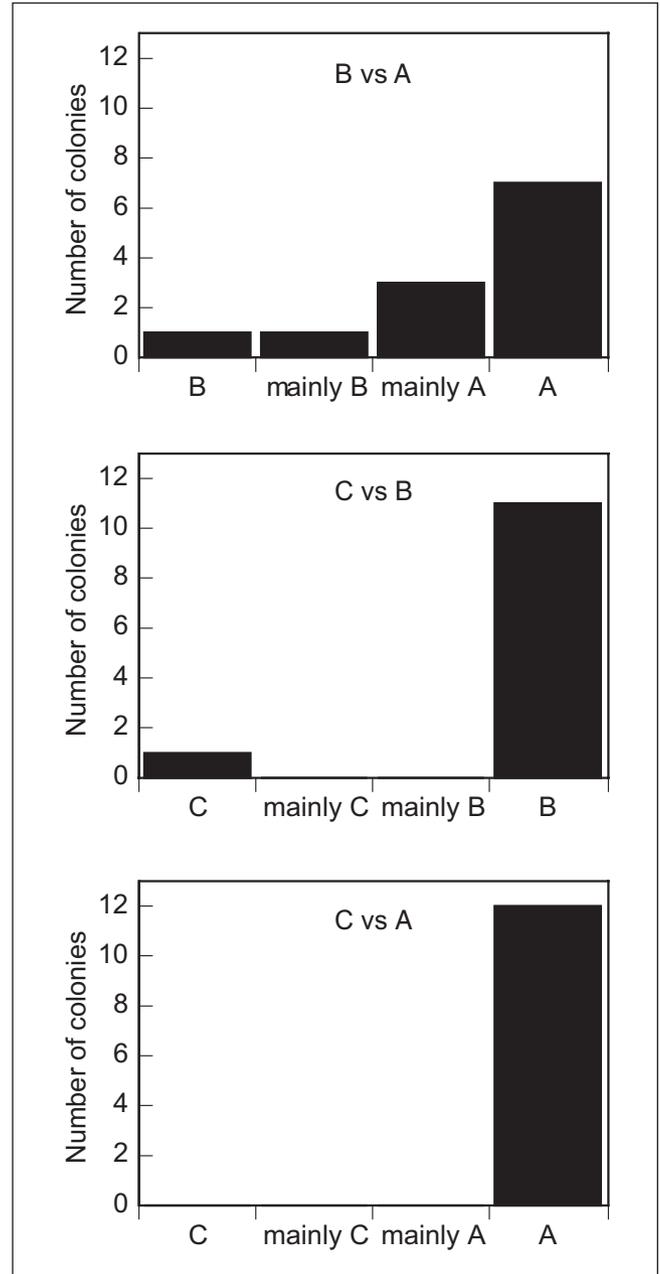


Fig. 1. Results of preference tests between pairings of nest designs A, B, and C. Bar heights give the number of colonies moving entirely into one nest or the other, or splitting between them.

available options and choose the better one, rather than use of mere satisficing. Decisions were usually unambiguous, but colonies split between candidate sites in 4 of the 36 emigrations.

Recruitment type and division of labor

Emigrations were divided into two distinct recruitment phases (Fig. 2). The first began after discovery of the new site by

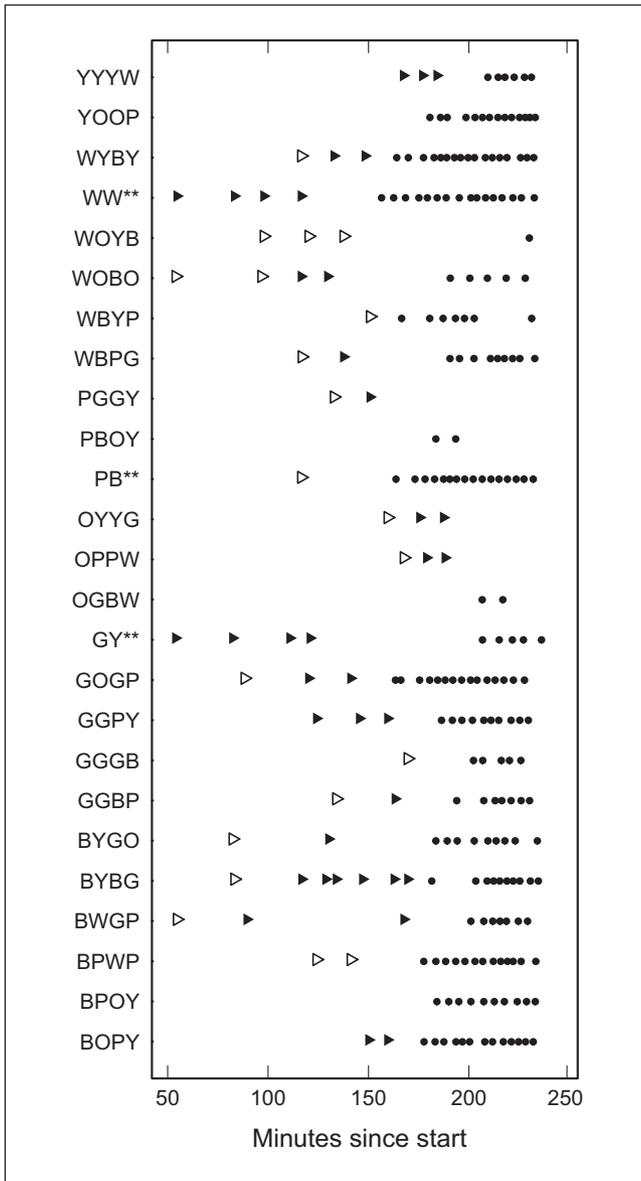


Fig. 2. Sequences of recruitment acts by each recruiter in a single emigration by colony 203. Each row shows the behavior of the ant named at the left. Closed triangles show when she led a tandem run to the new nest; open triangles when she followed a tandem run; and closed circles when she transported a nest mate. Times are relative to the removal of the roof of the old nest.

scouts from the damaged old nest, and consisted of a relatively small number of tandem runs leading from the old nest to the new. The second began later and consisted of a much larger number of transports bringing the bulk of the colony to the new site, sometimes interspersed with “reverse” tandem runs from the new nest to the old. This recruitment sequence was reflected in the behavior of individual recruiters: 65 ants first led tandem runs from the old nest and then switched to transport, 5 ants led tandem runs but never switched to transport, and 80 ants launched immediately into transport without first

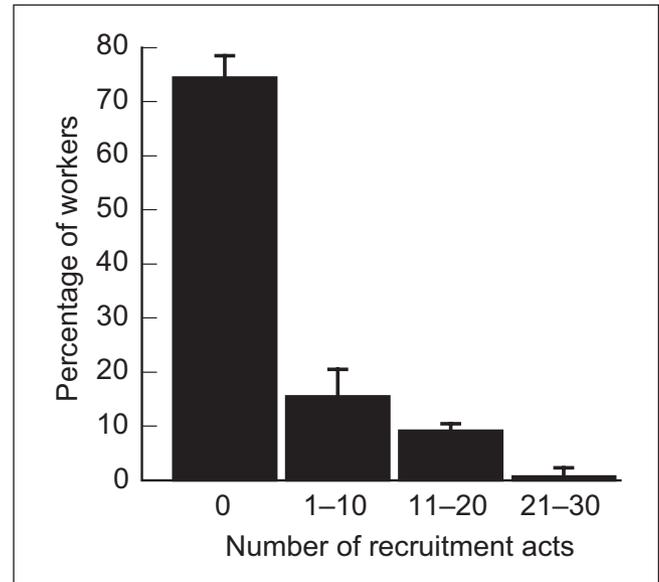


Fig. 3. Histogram of the number of recruitment acts performed by individual workers, averaged over six emigrations by three colonies. A total of 592 workers within emigrations were observed. Brackets show the standard deviation across emigrations.

leading tandem runs. In no case did an ant lead tandems from the old nest after starting to transport, but seven ants led occasional reverse runs, usually while returning to the old nest to gather a transportee. Ants that led forward tandem runs began recruitment consistently earlier than did pure transporters. Of the 70 tandem run leaders, 42 began recruitment before the earliest recruitment by a pure transporter, and all but 9 began before 20% of the pure transporters had started.

Within each emigration, most workers ($74.5 \pm 4.1\%$) never recruited (Fig. 3). Recruitment participation was strongly predicted by arrival type (Analysis of deviance: $\chi^2_{27} = 324, P < 0.001$), with followers and discoverers more likely than transportees to recruit (Fig. 4). Those transportees that did recruit were significantly more likely to be picked up in the arena (5 of 11 ants), compared to a random sample of non-recruiting transportees (1 of 11 ants) (Analysis of deviance: $\chi^2_1 = 3.9, P < 0.05$). Nest type had no influence on the proportion of ants recruiting (Analysis of deviance: $\chi^2_{28} = 0.18, P = 0.67$) nor on the number of recruitments by each recruiter (ANOVA on log-transformed data: $F^1_{144} = 0.43, P = 0.51$).

Recruitment speed

The mean round-trip duration of tandem runs (14.0 ± 10.6 min) was significantly longer than that of transports (5.7 ± 4.1 min; Wilcoxon test: $W = 121009, P < 0.001$, 112 tandems, 1198 transports). This difference stemmed partly from greater opportunities for learning during transport. Both types of recruitment grew faster with experience, but tandem runs were always concentrated at the start of an ant’s sequence of recruitments, and thus gained less than transports (Fig. 5).

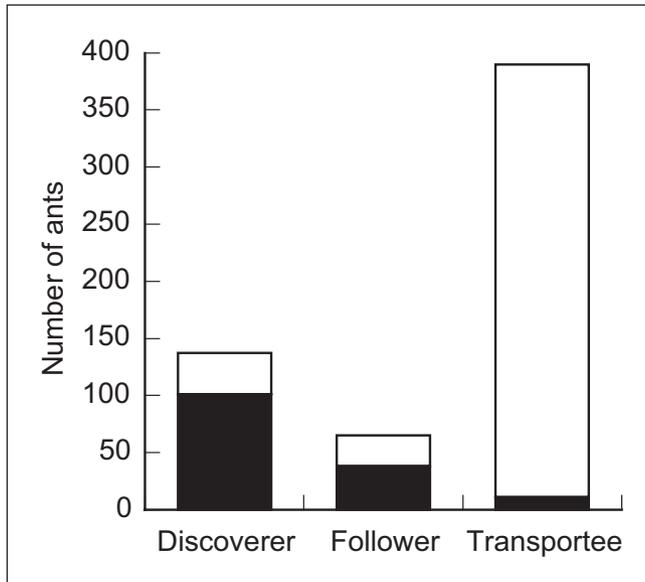


Fig. 4. Histogram of the route by which workers arrived at the new nest, pooled over six emigrations by three colonies. The shaded section of each bar shows the number of workers that recruited a nest mate in the course of the emigration.

When this effect was controlled for by modeling duration as a function of recruitment sequence, tandem runs were still significantly slower (ANOVA: $F_{1304}^1 = 9.6$, $P < 0.001$).

Nest-quality-dependent recruitment initiation

Active ants arriving at good nests started to recruit sooner than did ants arriving at mediocre nests (analysis of deviance: $\chi_1^2 = 24.0$, $P < 0.001$, $N = 208$; Fig. 6). The fitted rate for recruitment initiation at the good nest was $0.022 \pm 0.003 \text{ min}^{-1}$, corresponding to a mean latency of 44 minutes, while that for the mediocre nest was $0.010 \pm 0.001 \text{ min}^{-1}$, for a mean latency of 100 minutes. Separate analysis of each colony showed considerable variation in this difference, with a very strong effect of nest type on recruitment rate in colony 203 ($\chi_1^2 = 33.6$, $P < 0.001$, $N = 65$), a weak but insignificant effect in colony 205 ($\chi_1^2 = 2.8$, $P = 0.09$, $N = 70$), and little difference in colony 101 ($\chi_1^2 = 0.01$, $P = 0.91$, $N = 73$). Ants divided the latency period between visits to the new nest and journeys outside it. They made significantly more visits to mediocre sites (5.0 ± 3.5) than to good ones (3.0 ± 2.8 ; Wilcoxon test: $W = 3290$, $P < 0.001$).

Quorum rule

The probability of transporting, rather than leading a tandem run, rose sharply with nest population, reaching 50% at a mean population T of 5.8 ± 0.5 ants ($k = 1.7 \pm 0.3$) (Fig. 7). There was a significant difference, however, between first recruitment acts and later ones (ANOVA: colony: $F_{244}^2 = 11.5$, $P < 0.001$). The predicted value of T was 8.2 ± 0.8 , when

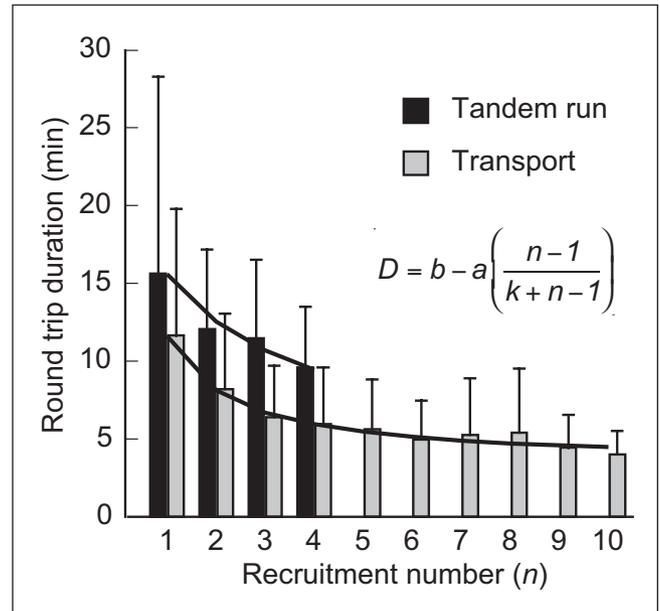


Fig. 5. Mean time to complete a recruitment journey as a function of recruitment experience, pooled over six emigrations by three colonies. Recruitment number indicates position within each ant's sequence of recruitment acts in a given emigration, regardless of recruitment type. Brackets show standard deviations. Lines connect values of the function shown, fit to the mean durations for each recruitment type (Tandem runs: $b = 15.6 \pm 1.2$; $a = 12.4 \pm 14.5$; $k = 3.1 \pm 6.4$; Transports: $b = 11.6 \pm 0.4$; $a = 8.2 \pm 0.4$; $k = 1.3 \pm 0.2$).

only the first recruitment decision of each ant was analyzed, and 4.1 ± 0.5 , when only later decisions were analyzed (Fig. 8A). This effect remained if decisions made at populations greater than 30 were excluded, to avoid any bias introduced by the preponderance of transports among first decisions at high populations (ANOVA: colony: $F_{217}^2 = 12.1$, $P < 0.001$). It also persisted if every decision was included, not just those deemed independent (ANOVA: colony: $F_{1309}^2 = 163.3$, $P < 0.001$). Nest type had no detectable influence on quorum size (ANOVA: nest: $F_{245}^1 = 0.53$, $P = 0.47$).

Scouts encountering a completely empty nest were significantly more likely to begin their recruitment with a tandem run, than were scouts encountering a populous nest (Analysis of deviance: $\chi_1^2 = 4.5$, $P < 0.05$; Table 1). When scouts in a populous nest were denied tactile contact with their nest mates, they behaved like ants in an empty nest, predominantly choosing to lead tandem runs. Considering all three treatments together, the opportunity for contact with nest mates in the cavity strongly predicted recruitment decision (Analysis of deviance: $\chi_1^2 = 8.8$, $P < 0.01$), while the population of the nest did not (Analysis of deviance: $\chi_1^2 = 0.16$, $P = 0.69$). Thus, in the absence of direct contact with nest mates in the cavity, ants responded as though the quorum had not been met, despite the availability of pheromonal or other indirect cues. There was some evidence for an effect of latency since an ant's discovery of the nest on her choice of recruitment method. Latencies were longer for ants choosing transport ($45.5 \pm 26.9 \text{ min}$) than for those choosing tandem

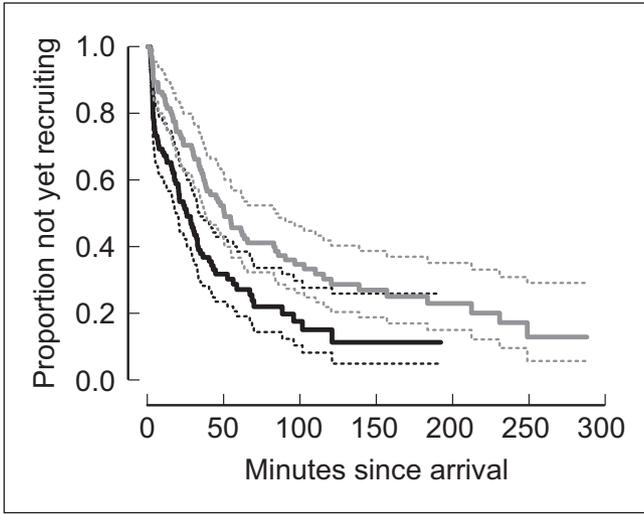


Fig. 6. The proportion of ants not yet recruiting, as a function of time since each ant first entered the new nest site, pooled over three colonies. Data are plotted separately for emigrations to good nests (black lines) and mediocre nests (gray lines). The solid lines show survival curves fit by the Kaplan-Meier method, and the dashed lines show the 95 % confidence interval for each survival curve.

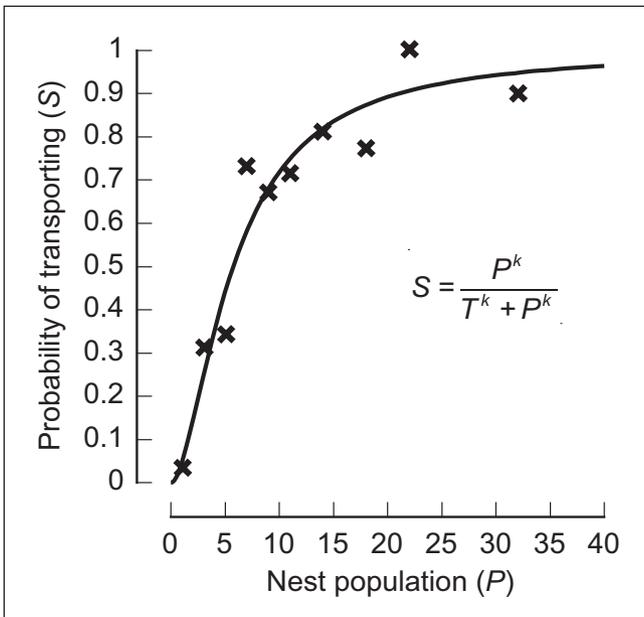


Fig. 7. Probability of a recruiter performing a transport rather than a tandem run, as a function of the number of other workers at the new site on her immediately previous visit there. Independent recruitment decisions were separated into bins on the basis of mean site population. Crosses show the proportion of decisions to transport within each bin. Each cross is at the midpoint of its bin. A total of 248 decisions were analyzed, the number in each bin ranging from 12 to 38. The line estimates transport probability as a Hill function fitted to these data ($T = 5.8 \pm 0.5$ ants; $k = 1.7 \pm 0.3$). Data are pooled from six emigrations by three colonies.

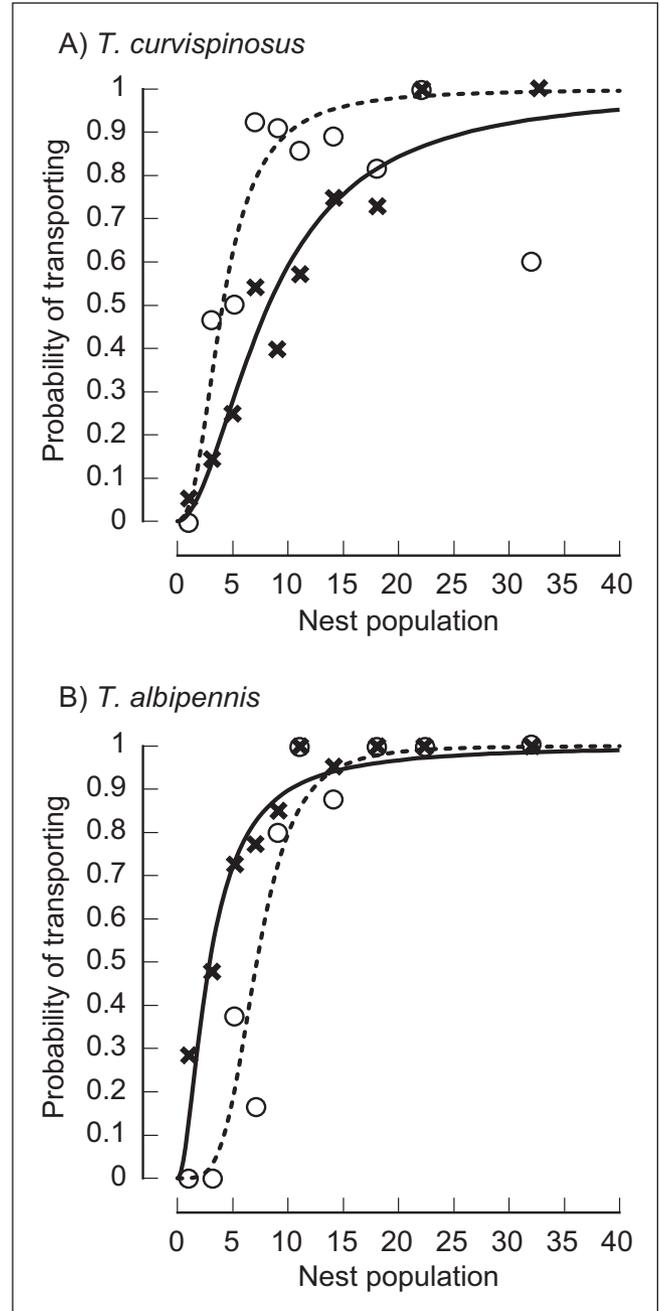


Fig. 8. Effect of recruitment timing on quorum size. Data and Hill function fit are plotted as in Fig. 7, but separately for the first recruitment of each ant (crosses and solid line) and all subsequent recruitments (open circles and dashed line). Data are pooled for A) six emigrations by *T. curvispinosus* and B) twelve emigrations by *T. albigennis*.

Table 1. The number of ants choosing either to transport or to lead a tandem run after discovering a nest in one of three conditions: empty of nest mates; nest mates present and freely accessible to direct contact; nest mates present but excluded from direct contact by a mesh barrier. The last row shows the mean nest population (exclusive of the discoverer) over all visits in each treatment.

	No Ants	Full contact	Ants/No Contact
Discoverers leading tandem runs	9	3	7
Discoverers transporting	2	6	0
Nest population	1.0 ± 0.6	15.1 ± 3.9	19.9 ± 4.3

runs (15.8 ± 27.7 min), and latency had a significant effect on recruitment choice, when tested independently of other factors (Analysis of deviance: $\chi^2_1 = 4.1$, $P < 0.05$). However, adding latency as an additional explanatory factor did not significantly improve the fit of a model based on opportunity for contact (Analysis of deviance: $\chi^2_1 = 2.2$, $P = 0.14$).

Quantitative comparison to *T. albipennis*

Most parameters characterizing the behavior of active ants differed significantly between the species (Table 2). For example, *T. albipennis* used a lower quorum size than *T. curvispinosus*, and also differed in the relation between quorum size and experience. While *T. curvispinosus* recruiters used a higher quorum on first than on later recruitment decisions, *T. albipennis* showed the opposite pattern (ANOVA: colony: $F^2_{432} = 19.9$, $P < 0.001$; Fig. 8B).

Parameter	<i>T. curvispinosus</i>		<i>T. albipennis</i>		P
	Estimate ± SE	N	Estimate ± SE	N	
Active Workers	0.45 ± 0.02	6	0.52 ± 0.02	12	0.15
1st TR duration	15.6 ± 0.8 min	110	15.1 ± 0.9 min	149	0.66
4th TR duration	9.3 ± 4.6 min		9.1 ± 1.4 min		
1st Trans duration	11.7 ± 0.7 min	1198	9.6 ± 0.6 min	1870	0.13
10th Trans duration	4.5 ± 0.98 min		4.4 ± 0.9 min		
Quorum _{all}	5.7 ± 0.5 ants	248	3.6 ± 0.3 ants	436	***
Quorum _{first}	8.2 ± 0.8 ants	147	2.9 ± 0.3 ants	383	***
Quorum _{later}	4.1 ± 0.5 ants	101	7.2 ± 0.7 ants	53	***
Recruit	0.26 ± 0.02 min ⁻¹	485	0.19 ± 0.01 min ⁻¹	729	***
PauseTrans	0.18 ± 0.15	231	0.25 ± 0.19	535	***
TransInNestTime	1.25 ± 0.04 min	1080	0.88 ± 0.01 min	1808	***
Reverse	0.01 ± 0.003	1219	0.06 ± 0.01	2050	***
PropLost	0.73 ± 0.04	98	0.83 ± 0.06	42	0.20
PickedUp	0.003 ± 0.0005 min ⁻¹	34	0.007 ± 0.0005 min ⁻¹	223	***

Table 2. Parameter estimates for an agent-based model of emigration behavior by *T. curvispinosus* and *T. albipennis*. Rightmost column shows significance of difference between species for each estimate. For tandem run (TR) and transport durations, sample sizes and P-values refer to a model fitting mean duration as a function of recruitment number.

Several measures pointed to slightly faster recruitment by *T. albipennis* workers. They were quicker to break off stays at the new nest in order to lead a tandem run or perform a bout of transports (Recruit), and they spent less time in the new nest between individual transport trips within a bout (TransInNestTime). On the other hand, *T. albipennis* workers more readily interrupted transport bouts to go on searches of the arena (PauseTrans), and did not complete individual recruitment journeys any faster than *T. curvispinosus* workers. A higher proportion of *T. albipennis* workers were active scouts, but this trend was not significant. A narrower measure of participation – the proportion of all workers actually recruiting per emigration – was significantly greater in *T. albipennis* (0.33 ± 0.08) than in *curvispinosus* (0.26 ± 0.04; $\chi^2_1 = 10.7$, $P < 0.01$).

T. albipennis scouts were more commonly picked up in the arena and carried to the new nest, and they were also more likely to lead reverse tandem runs. In both species, most followers of tandem runs lost contact with their leaders before arriving at the destination. The rate of such losses was higher in *T. albipennis*, but not significantly so.

Discussion

The emigration behavior of *T. curvispinosus* qualitatively resembles that of *T. albipennis*, despite showing many quantitative differences. In both species, colonies can actively choose among available options, rather than merely satisficing. Their decisions depend on an active minority of ants who look for potential new homes and use two methods to bring nest mates to promising finds: slow tandem runs to recruit fellow active ants, and faster transports of the colony's passive majority. Most importantly, active ants of both species

follow two key decision rules: 1) a site-quality dependent rate of recruitment initiation; 2) a quorum rule governing the switch from tandem runs to transports. Models of *T. albipennis* emigration have shown how these rules can contribute to efficient selection of the best nest (Pratt et al., 2002, 2005). A similar process appears to be at work in *T. curvispinosus*.

Individual decision rules

The effect of site quality on recruitment initiation reveals itself in the significantly longer delay between arrival at a mediocre site and first recruitment to it, compared to the corresponding latency at a good site. Evidence for the quorum rule is less forthcoming from observations on unmanipulated ants. Support is found in the positive relationship between site population and probability of transport, but this pattern is equally consistent with the alternative hypothesis that an autonomous program dictates a brief period of tandem running followed by transports. The apparent link to population could be a simple consequence of population growth over the course of an emigration, so that an ant's early recruitment acts will tend to be made to a relatively empty nest. The critical test distinguishing these hypotheses is the behavior of first-time recruiters at sites manipulated to have either few or many ants. Under the autonomy hypothesis, there should be no difference in the recruitment decisions observed in each treatment. Under the quorum hypothesis, ants at the empty site should be more likely to lead tandem runs. The latter is exactly what happens, showing clearly that ants base their recruitment decisions at least partly on a quorum rule.

How does a recruiter perceive the number of ants in the new nest? The necessity of direct contact is apparent in the consistent choice of tandem runs by ants denied contact with nest mates in a populous site. Recruiters of *T. albipennis* behave similarly, and have further been shown to rely on the rate of tactile encounters among ants, implying that they respond to nest mate density rather than absolute population (Pratt, 2005). Further experiments are needed to determine whether the same is true for *T. curvispinosus*. In addition, there is evidence for a small additional effect of latency, opening the possibility that ants grow "impatient" and become increasingly likely over time to begin transport, regardless of site population. This idea also awaits more direct experimental test.

Speed vs. accuracy of decision-making

The ants' decision strategy can be summarized as an investment of time to gain information. When a scout delays recruitment to a site she has found, she retards the colony's emigration, but improves its chances of ending up in the best available nest. This improvement has several sources: the chance that she herself will find a better candidate while she hesitates; the even greater chance that one of her many nest mates will do so; and the likelihood that any superior site already found by a nest mate will experience recruitment soon-

er, due to higher initiation rates at better sites. In the same way, ants slow emigration when they put off rapid transport in favor of further tandem runs. In exchange, they enhance decision accuracy by integrating the independent assessments of several scouts, and by amplifying the differences in recruitment rate at sites of different quality (Pratt et al., 2002).

The inherent trade-off between decision speed and accuracy might explain some quantitative variation in the ants' decision rules. For example, colonies varied widely in the effect of site quality on recruitment initiation rate, from highly significant to undetectable. When ants initiate recruitment nearly as rapidly to a mediocre site as to a good one, this implies unwillingness to pay a time cost to ensure selection of the better site. One factor that can encourage such unwillingness is the severity of conditions at the old nest. Colonies of both *T. albipennis* and *T. curvispinosus* respond to increasing severity by accelerating their emigrations, at the cost of decision accuracy (Dornhaus et al., 2004; Franks et al., 2003a). For *T. curvispinosus*, this response has been partly traced to a sharp increase in the recruitment initiation rates of individual ants (pers. obs.). In extreme crises, ants may simply start recruiting as fast as possible to any site better than their current one. In the emigrations analyzed here, all colonies faced identical conditions at the old nest; hence variation in severity cannot explain differences in emigration behavior. Colonies may vary, however, in the relative emphasis they place on speed vs. accuracy, leading to different responses in similar circumstances.

Interspecific comparisons

Speed-accuracy trade-offs are also relevant to some of the quantitative differences between *T. curvispinosus* and *T. albipennis*, such as the latter's lower quorum size. Within both species, the same urgent conditions that encourage faster recruitment initiation also reduce quorum size (Dornhaus et al., 2004; Franks et al., 2003a). By accelerating the switch to rapid transport, this change increases the speed with which the old nest is abandoned, but it also impairs decision accuracy. If variation in quorum size across species has the same implications, it is possible that *T. albipennis*, at least within the emigration contexts examined here, places relatively greater emphasis on speed of emigration than on decision accuracy.

A potentially related difference lies in the effect of recruitment experience on quorum size. In *T. curvispinosus*, ants demand a larger population to launch immediately into transport than they do when switching to transport after first leading one or more tandem runs. This is apparent in the leftward shift of the function linking transport probability to site population, for later vs. initial recruitment decisions (Fig. 8A). This suggests that ants have a tendency to begin their recruitment with a tandem run, and only relatively high site population can overcome this bias. Once they have begun leading tandem runs, however, a behavioral momentum urges them to switch to transports, even at relatively low populations. *T. albipennis* shows exactly the opposite pattern, with low initial quorums increasing after the first tandem run (Fig.

8B). This result is consistent with a tendency toward speedier emigration by *T. albipennis*, because the especially low early quorum will lead to the very early onset of transport. On the other hand, it also implies that those ants beginning with tandem runs tend to continue with them, even as site population increases and newcomers move directly into transport.

Other interspecific differences also point to a greater emphasis on speed by *T. albipennis*. They invest a greater proportion of colony labor in emigration, with a trend toward more scouts and a significantly larger proportion of recruiters. They also initiate recruitment bouts more rapidly and spend less time in the new nest between transports. A possible exception to this pattern is the greater rate at which they interrupt transport bouts to explore the arena, which may be interpreted as a diversion of effort from rapid movement to search for other sites. However, an alternative explanation is that these pauses reflect a greater tendency by *T. albipennis* to lose their way while traveling between sites. This is consistent with their higher rate of failed tandem runs, when leader and follower become separated before reaching their destination. It is also consistent with the higher rate at which *T. albipennis* scouts are picked up in the arena and carried to the new nest. Transports originating in the arena appear to be directed at active ants that have gone astray and need retrieval by better-oriented nest mates. These interspecific differences do not necessarily reflect variation in intrinsic navigation ability. Workers of *T. albipennis* may simply have suffered from a lack of conspicuous visual landmarks like those provided for *T. curvispinosus*. These and other *Temnothorax* species use visual cues for orientation (Aron et al., 1988; McLeman et al., 2002; Pratt et al., 2001), hence their navigation may deteriorate in a visually featureless environment.

Given the narrow range of emigration contexts so far examined, it will be important to determine how consistently these species differ over a wider array of circumstances more accurately reflecting the kinds of challenges they face in nature. These include larger numbers of potential sites, a greater diversity of site qualities, longer distances among sites, and a wider range of levels of emigration urgency. It is also important to keep in mind the interesting possibility that much observed variation reflects no functional difference at all. Instead, parameter values may be only loosely regulated, and thus subject to large random variation among samples. Natural selection may have shaped a decision algorithm that works reliably not because it is governed by precisely regulated individual behavior, but because its structure grants it a high degree of robustness to variation in this behavior. With the detailed quantitative data available from these ants, future work can determine the respective roles in their decision algorithms of robustness to environmental variability and adaptation to specific emigration circumstances.

Acknowledgments

This work was supported by the Pew Charitable Trusts (award 2000-002558). I thank David Sumpter for extensive comments that improved an earlier version of the manuscript.

References

- Aron S., Deneubourg J.L. and Pasteels J.M. 1988. Visual cues and trail-following idiosyncrasy in *Leptothorax unifasciatus*: an orientation process during foraging. *Insect. Soc.* 35: 355–366
- Camazine S., Deneubourg J.L., Franks N.R., Sneyd J., Theraulaz G. and Bonabeau E. 2001. *Self-organization in Biological Systems*. Princeton University Press, Princeton, N.J. 538 pp
- Dornhaus A., Franks N.R., Hawkins R.M. and Shere H.N.S. 2004. Ants move to improve: colonies of *Leptothorax albipennis* emigrate whenever they find a superior nest site. *Anim. Behav.* 67: 959–963
- Franks N.R., Dornhaus A., Fitzsimmons J.P. and Stevens M. 2003a. Speed versus accuracy in collective decision making. *Proc. R. Soc. London, 270B*: 2457–2463
- Franks N.R., Mallon E.B., Bray H.E., Hamilton M.J. and Mischler T.C. 2003b. Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* 65: 215–223
- Franks N.R., Pratt S.C., Mallon E.B., Britton N.F. and Sumpter D.J.T. 2002. Information flow, opinion polling and collective intelligence in house-hunting social insects. *Phil. Trans. R. Soc.* 357B: 1567–1583
- Hirsh A.E. and Gordon D.M. 2001. Distributed problem solving in social insects. *Ann. Math. Artif. Intel.* 31: 199–221
- Langridge E.A., Franks N.R. and Sendova-Franks A.B. 2004. Improvement in collective performance with experience in ants. *Behav. Ecol. Sociobiol.* 56: 523–529
- Mailleux A.C., Deneubourg J.L. and Detrain C. 2003. Regulation of ants' foraging to resource productivity. *Proc. R. Soc. London, 270B*: 1609–1616
- Mallon E.B. and Franks N.R. 2000. Ants estimate area using Buffon's needle. *Proc. R. Soc. London, 267B*: 765–770
- Mallon E.B., Pratt S.C. and Franks N.R. 2001. Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* 50: 352–359
- McCullagh P. and Nelder J.A. 1989. *Generalized Linear Models*. Chapman and Hall, New York. 511 pp
- McLeman M.A., Pratt S.C. and Franks N.R. 2002. Navigation using visual landmarks by the ant *Leptothorax albipennis*. *Insect. Soc.* 49: 203–208
- Möglich M. 1978. Social organization of nest emigration in *Leptothorax* (Hym., Form.). *Insect. Soc.* 25: 205–225
- Pratt S.C. 2005. Quorum sensing by encounter rates in the ant *Temnothorax albipennis*. *Behav. Ecol.* 16: 488–496
- Pratt S.C. and Pierce N.E. 2001. The cavity-dwelling ant *Leptothorax curvispinosus* uses nest geometry to discriminate between potential homes. *Anim. Behav.* 62: 281–287
- Pratt S.C., Brooks S.E. and Franks N.R. 2001. The use of edges in visual navigation by the ant *Leptothorax albipennis*. *Ethology* 107: 1125–1136
- Pratt S.C., Mallon E.B., Sumpter D.J.T. and Franks N.R. 2002. Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* 52: 117–127
- Pratt S.C., Sumpter D.J.T., Mallon E.B. and Franks N.R. 2005. An agent-based model of collective nest site choice by the ant *Temnothorax albipennis*. *Anim. Behav.* 70: 1023–1036
- Seeley T.D. 1995. *The Wisdom of the Hive*. Belknap Press of Harvard University Press, Cambridge, Massachusetts. 318 pp
- Seeley T.D. and Visscher P.K. 2004. Group decision making in nest-site selection by honey bees. *Apidologie* 35: 101–116
- Theraulaz G., Gautrais J., Camazine S. and Deneubourg J.L. 2003. The formation of spatial patterns in social insects: from simple behaviours to complex structures. *Phil. Trans. R. Soc.* 361A: 1263–1282
- Todd P.M. and Gigerenzer G. 2000. Precise of Simple heuristics that make us smart. *Behav. Brain Sci.* 23: 727–780
- Venables W.N. and Ripley B.D. 2002. *Modern Applied Statistics with S*. Springer, New York. 495 pp