

Stephen C. Pratt · Eamonn B. Mallon
David J. T. Sumpter · Nigel R. Franks

Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*

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Abstract When its nest is damaged, a colony of the ant *Leptothorax albipennis* skillfully emigrates to the best available new site. We investigated how this ability emerges from the behaviors used by ants to recruit nestmates to potential homes. We found that, in a given emigration, only one-third of the colony's workers ever recruit. At first, they summon fellow recruiters via tandem runs, in which a single follower is physically led all the way to the new site. They later switch to recruiting the passive majority of the colony via transports, in which nestmates are simply carried to the site. After this switch, tandem runs continue sporadically but now run in the opposite direction, leading recruiters back to the old nest. Recruitment accelerates with the start of transport, which proceeds at a rate 3 times greater than that of tandem runs. The recruitment switch is triggered by population increase at the new site, such that ants lead tandem runs when the site is relatively empty, but change to transport once a quorum of nestmates is present. A model shows that the quorum requirement can help a colony choose the best available site, even when few ants have the opportunity to compare sites directly, because recruiters to a given site launch the rapid transport of the bulk of the colony only if enough active ants have been "convinced" of the worth of the site. This exemplifies how insect societies can achieve adaptive colony-level behaviors from the decentralized interactions of relative-

ly poorly informed insects, each combining her own limited direct information with indirect cues about the experience of her nestmates.

Keywords Decentralized control · Emigration · Recruitment · Transport · Quorum sensing

Introduction

The emigration of an insect society demands an exceptional degree of coordination among colony members. At a minimum, the colony must find a suitable nest site and safely bring its entire population there. Typically, it must also evaluate several potential sites, compare them, and choose the best one. Furthermore, the colony must reach consensus on a single site, rather than splitting its members among several. Recent work has shown that honey bees and ants can achieve these ends without any form of central control (Camazine et al. 1999; Seeley and Buhrman 1999; Visscher and Camazine 1999; Mallon et al. 2001). The society instead functions as a single information-processing unit, distributing its cognitive tasks across a multitude of workers. This ability, evident in many aspects of social insect behavior, makes them leading examples of decentralized control in biology (Tofts and Franks 1992; Seeley 1995; Bonabeau et al. 1997; Pratt 1998; Gordon and Hirsh 2001). The challenge in understanding these systems is to trace the links between the behavioral rules and information sources guiding individual insects, and the cognitive abilities of the colony as a whole.

Here we address this problem in the context of emigrations by the ant *Leptothorax albipennis*. These ants form small colonies (fewer than 500 workers) that typically nest in thin rock crevices whose fragility is likely to require frequent emigrations (Partridge et al. 1997). In the laboratory, ants can readily be induced to move from one artificial nest to another by opening the old nest and providing an intact new one nearby (Sendova-Franks and Franks 1995). A curious aspect of the ants' behavior dur-

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S.C. Pratt (✉) · E.B. Mallon · N.R. Franks
University of Bath, Department of Biology and Biochemistry,
Bath BA2 7AY, UK

D.J.T. Sumpter
Centre for Mathematical Biology, Mathematical Institute,
Oxford University, 24–29 St Giles', Oxford OX1 3LB, UK

Present addresses:
S.C. Pratt, Department of Ecology and Evolutionary Biology,
Princeton University, Princeton, NJ 08544, USA,
e-mail: spratt@princeton.edu, Fax: +1-609-2581334

N.R. Franks, School of Biological Sciences, University of Bristol,
Woodland Road, Bristol BS8 1UG, UK

ing these emigrations is their reliance on two distinct methods of bringing nestmates to the new site. They begin by leading tandem runs, in which a recruiter slowly leads a single ant from the old nest to the new (Möglich et al. 1974; Möglich 1978). Later, tandem runs give way to transports, in which ants simply pick up nestmates and carry them to the new site. Transports are far more numerous than tandem runs, and are used to summon the bulk of the colony. Interestingly, although transports replace tandem runs from the old nest, they are often accompanied by “reverse” tandem runs from the new nest to the old.

Why should the ants use two methods of recruitment? Möglich (1978), working with other *Leptothorax* species, proposed that the initial tandem-running phase serves as “recruitment of recruiters”. That is, tandem runs recruit a corps of ants who later transport the rest of the colony. Division of labor between a minority of active movers and a majority of passive ants is typical of many ants (Möglich and Hölldobler 1974, 1975; Abraham and Pasteels 1980), including at least one *Leptothorax* species (Sendova-Franks and Franks 1995). Moreover, Möglich (1978) found that the rate of emigration increased as the colony switched to transport, consistent with an enlargement of the population of recruiters. However, this hypothesis has yet to be directly tested by tracking the behavior of individually identifiable tandem run followers and transportees. The role of reverse tandem runs also remains completely unexplained.

A related mystery is how individual recruiters decide which method to use. One possibility is that ants follow a stereotyped program, always leading a few tandem runs from the old nest and then switching automatically to transport and reverse tandem runs. Evidence for more flexible decision-making comes from behavior during laboratory emigrations over very short distances (Sendova-Franks and Franks 1995). In these cases, the initial tandem running phase is often completely absent, suggesting that the length or difficulty of the emigration route may affect the choice of recruitment method.

More intriguingly, if tandem runs serve to summon recruiters, ants may switch to transport only when they sense that a quorum of nestmates is present at the new site. Not only could this rule ensure enough recruiters, it could also play a role in a colony’s collective decision among several potential sites. *Leptothorax* show clear preferences for certain nest designs over others, and will reliably emigrate to the better site if presented with two of different quality (Mallon and Franks 2000; Mallon et al. 2001; Pratt and Pierce 2001). The colony’s decision springs in part from scouts that visit both sites and subsequently recruit only to the better one (Mallon et al. 2001). Many ants, however, visit only one site, and their contribution to the colony’s choice is instead made through a simple decision rule. Namely, they initiate recruitment after a delay that is inversely proportional to the quality of the site (Mallon et al. 2001). As a result, the positive feedback engendered by recruitment increases the population more rapidly at superior sites.

This distributed process suffers from a major weakness, in that it cannot prevent ants from moving some workers and brood to an inferior site. To avoid a permanent split, these items must later be transferred to the preferred site, incurring additional costs in time and risk of exposure. Thus, the colony should benefit from any individual behavior that reduces the likelihood of transports to worse sites. Waiting for a quorum of nestmates before initiating transport might have such an effect, by making rapid, large-scale transport conditional on “convincing” a sufficient number of recruiters of the appeal of a given site.

In this paper, we examine the roles of tandem running and transport in colony emigration. We begin by studying videotaped emigrations of individually marked ants, to show that moves are organized by a minority of active scouts and recruiters. We then show that these active ants first use slow tandem runs to recruit other active ants to promising finds, but later switch to faster transports of passive ants and brood items. Next, we experimentally test the hypothesis that an ant’s initial choice of recruitment method depends on site population, with tandem runs chosen for low populations and transports preferred once a quorum of nestmates is present. We compare this to the alternative explanation that the choice depends only on the distance over which the ant must recruit. In another experiment, we test the related hypothesis that an ant that has begun by leading tandem runs switches to transport only when a quorum is filled. We compare this to the alternative possibility that she instead leads a roughly constant number of tandem runs before switching automatically to transport. Finally, we develop a model, based on our empirical results, to show how a quorum requirement can help a colony efficiently choose between two sites of different quality, by supplementing each ant’s limited direct experience with indirect cues about the experience of her nestmates.

Methods

Ants, observation nests, and marking

Seven colonies of *L. albipennis* were collected in July 1998, March 1999, and February 2000 at Portland Bill in the United Kingdom (50°32’N, 2°27’W). Colonies were housed in observation nests made by sandwiching a cardboard perimeter between two large microscope slides (50×76 mm). Because the thin nest cavity (33×25×1.6 mm) could accommodate only a single layer of ants, the nest’s transparent roof offered an unobstructed view of every ant. Each nest rested in a petri dish that served as a foraging arena, accessible to the ants through a small hole in the nest wall. In the arena, colonies were fed ad libitum on *Drosophila* and dilute honey. The arena walls were coated with Fluon to prevent the ants from escaping. All colonies had a single queen. Worker populations ranged from 40 to 150, and brood populations from 5 to 200.

To allow tracking of individual behavior during emigrations, all of the workers in each colony received distinctive combinations of paint marks on the head, thorax, and gaster (see Sendova-Franks and Franks 1993 for details of the painting technique).

Induction of emigrations and videotaping methods

To generate a thorough description of recruitment behavior, we videotaped 12 complete emigrations (2 by each of 6 marked colonies). For each emigration, an occupied nest was transferred to a large Plexiglas tray (75×43×7 cm), the walls of which were coated with Fluon. The nest was placed against the center of one wall of the tray, with an empty new nest 65 cm away against the opposite wall. A digital video camcorder (Panasonic NV-DS1 or JVC GRDV3ek) mounted on a copy stand was positioned approximately 10 cm above the new nest. The camera's field of view was adjusted to encompass the entire nest interior, as well as a 1- to 3-mm strip immediately in front of the entrance. In the two emigrations by colony 6, a camera was similarly positioned above the old nest.

Emigrations were induced by removing the upper slide from the old nest, stimulating the exposed ants to seek out a new home. Videotaping began at the start of emigration and continued until all adults and brood items, barring a few scouts, were inside the new nest. Throughout the emigration, the start and end times and the participants of tandem runs that occurred out of camera range were noted by an observer and recorded on the audio channel of the videotape. Other data from these emigrations are reported in Mallon et al. (2001).

At the time of videotaping, 15±12% of ants were unmarked, some because they had lost their marks, but most because they had eclosed from pupae after the marking period. We rarely observed recruitment by these recently eclosed workers; hence their presence did not prevent us from identifying nearly all active recruiters.

In addition to the 12 main emigrations, we induced 2 further moves by colony 1, once with a separation of 10 cm between the nests, and once with a separation of 60 cm. These data helped us to determine whether emigration distance has any effect on the incidence of forward tandem runs. The short emigration was staged in a square petri dish (22×22×1.7 cm) and the long emigration in a large plastic tray (74×49×8 cm). Induction of emigration and videotaping methods were otherwise identical to those described above.

During playback of the videotapes, we recorded: (1) the time of every entry and exit at the new nest site, and the identity of the ant; (2) the time at which each transporter arrived at the new nest, and the identity of both transporter and transportee; (3) the start and end times of each tandem run, the direction of the run, and the identity of leader and follower. We wrote a series of programs in C++ to extract summaries of this raw data for the plots and analyses described in detail below and in the results section.

We estimated colony population at each emigration by counting the individually identifiable ants recorded on the videotape. We then added the number of unmarked ants brought to the new nest by the end of the emigration. Brood populations were estimated for each emigration by counting the number of transports required to move all of the colony's brood to the new nest.

Recruitment rate

To determine the colony's recruitment rate over a given time interval, we measured the change in population at the new site during the interval, and divided it by the interval length. To determine per capita recruitment rate, we measured, for each recruiter, the mean duration from the beginning of one recruitment act to the beginning of the next. We then took the mean of these values over all recruiters in each emigration. To measure the speed at which recruiters crossed the arena, we divided the distance between the nests by the time taken by each recruiter to traverse it. Crossing speed was assayed only for the two emigrations by colony 6, in which simultaneous videotaping of both the old and new nests allowed precise measurement of traversal duration.

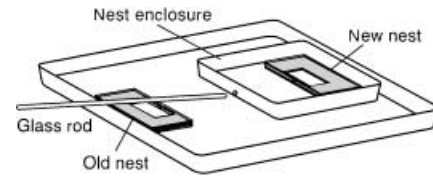


Fig. 1 Emigration arena used to control population of new nest site

Experimental analysis of factors affecting recruitment method

Emigration arena

We designed an arena that allowed us to manipulate the population of the new nest independently of emigration distance, in order to disentangle the effects of these factors on recruitment type (Fig. 1). The old and new nests lay 10 cm apart on opposite sides of a large petri dish (22×22×1.7 cm). The new nest rested inside a smaller petri dish (10×10×1.7 cm) that the ants could enter only through a tiny hole (3 mm diameter). Passage in and out of the small dish could be controlled by temporarily plugging the hole with the rounded tip of a glass rod. In this way we could sharply reduce the high discovery rate and rapid population growth normally associated with a short emigration distance. Alternatively, we could augment the nest population independently of discovery rate, by moving ants directly to the enclosure.

Initiation of recruitment

To determine whether high population at the new nest site induces ants to launch immediately into transport, without first leading tandem runs, we compared the number of tandem runs led by colonies under two treatments. In the Low treatment, the number of scouts allowed into the enclosure was restricted, to ensure a low new nest population when the ants began to recruit. In the High treatment, 15 adult workers were directly transferred from the old nest at the start of emigration, to ensure a high new nest population at the time of first recruitment. The ants were gently lifted with a fine paint brush and deposited inside the enclosure. The dish was closed to all discoverers for 20 min, so that the transferred ants could recover from the disturbance and find their way into the new nest.

In both treatments, the first scout to find the nest site was permitted to enter and leave the dish at will, but no other ant was allowed in. If the first discoverer failed to recruit within 1 h of her first entry into the new nest, she was denied further access to the dish, and a new scout was allowed to enter. Access to the enclosure remained restricted to the initial scout and her recruits, until their number made effective control impossible. Thus the emptiness of the nest in the Low treatment was gradually eroded by recruitment and further discoveries, but it persisted long enough to create a meaningful contrast with the High treatment.

Induction of emigrations and videotaping proceeded as described above. Because this experiment addressed only the individual choices made at the start of recruitment, taping stopped once the emigration had clearly entered the transport phase; that is, when the transportation rate was high, and when all forward tandem leaders had switched to transport. Each of four colonies received four replicates of each treatment.

Maintenance of tandem running

To discover whether an increase in nest population is necessary for a tandem leader to switch to transport, we performed an experiment that severed the normal link between tandem running and population growth. Only a single discoverer was allowed into the new nest site, as described above. Once she began to lead tandem

runs, we prevented her recruits from entering the new nest by carefully aspirating them as they came within 1 cm of the nest entrance. If the removal alarmed the tandem leader, we aborted the experiment. Alarmed ants were easy to detect, because they ran rapidly and agitatedly, in contrast to isolated tandem run leaders, who stood still for several seconds, waiting for their followers to re-establish contact. We continued removing followers until the recruiter began transporting, or until at least 3 h had passed since her first tandem run. We repeated this experiment eight times, on ants from four different colonies.

We compared the number of tandem runs led by each ant, and the duration until she switched to transport, with the same figures for recruiters in the Low treatment of the Initiation experiment. For those ants that never switched to transport, we conservatively estimated the duration until first transport as the total observation time since the first tandem run.

Statistical analysis

All statistical analyses were carried out with SPSS 10 on Macintosh computers. Data that were heteroscedastic or not normally distributed were either log-transformed or analyzed with appropriate nonparametric methods, as described below. All measurements are reported as mean±standard deviation.

Results

Sequence of recruitment methods

Of the 12 emigrations, 9 passed through 3 distinct phases, separated by changes in recruitment behavior. In the first phase, scouts dispersed throughout the arena, where some of them discovered the new nest and began to evaluate it. The second phase began when one of these scouts led a tandem run from the old nest to the new, 58 ± 23 min after the start of emigration. During this phase, further tandem runs, as well as continued independent discoveries, slowly increased the number of visitors to the new site. The third phase began with the first transport, 47 ± 61 min after the first tandem run. After a lag of 25 ± 17 min, forward tandem runs gave way completely to transports, accompanied by reverse tandem runs from the new nest back to the old. Population growth at the new site accelerated in the third phase, and the entire colony was moved to the new nest within 95 ± 42 min. The remaining three emigrations showed a similar pattern, except that the early tandem-running phase was absent.

The behavioral trajectories of individual recruiters fell into two distinct classes. A minority ($10\pm 9\%$, $n=12$) led a few tandem runs before switching completely to transport (or, in two cases, abandoning recruitment altogether). The remainder led no forward tandem runs, instead launching immediately into transport. Despite these differences, the colony as a whole still showed a clear division between tandem run and transport phases. This is because ants that led no forward tandems began their recruitment later, so that their efforts coincided with the transport phase of the tandem runners.

Reverse tandem runs occurred sporadically throughout the transport phase in 9 of the 12 emigrations, and were typically led by active transporters on their way

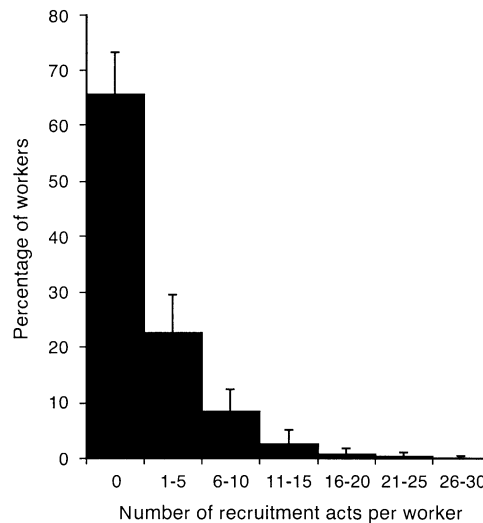


Fig. 2 Distribution of recruitment effort across ants. Bars give the mean and standard deviation across 12 emigrations of the percentage of the worker population performing a given number of recruitment acts

back to the old nest to retrieve a nestmate. Of the 8 ± 3 reverse tandem leaders in each of these nine emigrations, $99\pm 4\%$ also recruited from the old nest, and $84\pm 16\%$ of reverse tandems ended with the leader picking up an adult or brood item for retrieval. This suggests that leaders were attempting to induce idle workers at the new site to join them in taking items from the old nest. Consistent with this hypothesis, $73\pm 13\%$ of the 10 ± 9 followers in each emigration themselves actively recruited from the old nest. If reverse tandems served to stimulate recruitment, however, they were often redundant, since $53\pm 15\%$ of recruiting followers had already started to recruit before following a reverse tandem run.

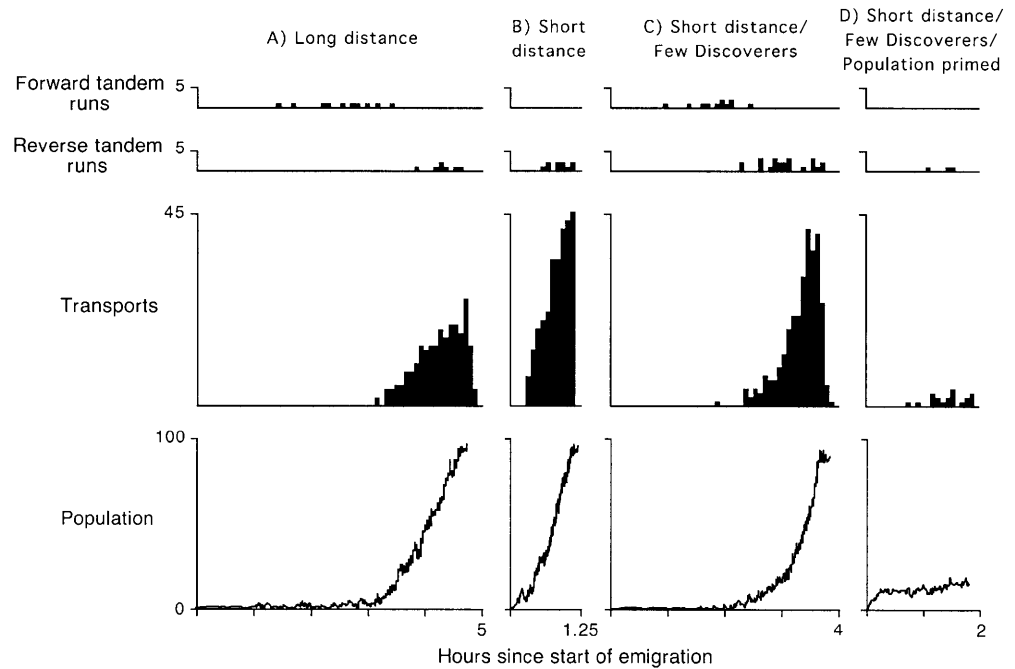
Division of labor

Recruitment effort was very unevenly distributed, with $65\pm 8\%$ of ants in each of the 12 emigrations performing no tandem runs or transports whatsoever. Among those that did recruit, variation in effort was high (Fig. 2). Only $12\pm 3\%$ of recruiters were responsible for 25% of all recruitment acts, and $26\pm 5\%$ accounted for half of all recruitment acts. In absolute terms, 34 ± 11 ants out of a total population of 99 ± 34 recruited at least once, and moved a total population of 208 ± 95 , including 108 ± 64 brood items.

Correspondence between recruitment type and subsequent role

If forward tandem runs serve to summon a corps of recruiters, then tandem followers should take up recruitment at a disproportionate rate, compared to transportees. To test this prediction, we classified each ant into

Fig. 3A–D Time course of recruitment behavior and population growth in four emigrations by colony 1. **A** 60 cm emigration; **B** 10 cm emigration; **C** 10 cm emigration with the number of discoverers restricted; **D** 10 cm emigration with the number of discoverers restricted, and with priming of the new site's population at the start of emigration. Each bar in the histograms shows the number of recruitment acts during a 5-min period. Fewer acts are shown in *panel D* because observation ceased once the transport phase was well under way



one of three groups, depending on how she first arrived at the new nest: (1) transportees were carried into the nest; (2) followers followed a tandem run toward the new nest, and then walked in; (3) discoverers walked into the new nest without first following a tandem run. As predicted, arrival type corresponded strongly to subsequent recruitment activity (G test: $G=302$, $P<0.001$; $n=994$). Seventy-one percent of discoverers and 60% of followers later recruited, compared to only 17% of transportees. Moreover, transportees that became recruiters differed from those that remained passive. Examination of the 2 emigrations by colony 6 in which data were collected simultaneously at the old and new nests shows that only 8 of 36 transports of future recruiters began at the old nest, compared to 61 of 81 transports of passive ants (G test: $G=29.7$, $P<0.001$; $n=117$). Active ants were presumably picked up while walking in the arena, behavior consistent with their scouting for nest sites.

Recruitment rate

Recruitment rate increased significantly as colonies switched from tandem runs (0.34 ± 0.27 items/min) to transports (1.68 ± 0.9 items/min) (ANOVA: $P<0.001$, $n=12$ emigrations). Recruitment accelerated partly because more ants participated (transport phase: 33 ± 11 ; tandem phase: 3 ± 3), and partly because the per capita rate of recruitment was 3 times greater for transports (0.099 ± 0.02 min $^{-1}$) than for tandem runs (0.033 ± 0.016 min $^{-1}$) (ANOVA: $P<0.001$, $n=12$ emigrations). Much of this difference lay in the greater speed at which transporters crossed the arena (4.6 ± 2.2 mm/sec, $n=387$) compared to tandem run leaders (1.5 ± 0.65 mm/sec, $n=14$) (Wilcoxon signed ranks: $P<0.001$). Tandem runs

lost time because they frequently split up, requiring the leader to stand still and wait for the follower to find her again.

Effect of nest population on choice of recruitment method

Recruiters fell into two groups – those that switched from tandem runs to transport, and those that only transported. This suggests that their decision-making can be broken into two distinct questions. First, when an ant initiates recruitment, how does she choose between tandem running and transport? Second, for those ants that begin by leading tandem runs, how do they decide when to switch to transport?

Initiation of recruitment

We considered two hypotheses for the initial choice of recruitment method: (1) an ant's decision depends on the distance over which she must recruit, with tandem runs chosen only for relatively long emigrations; (2) the decision depends on the number of nestmates at the new site, with ants choosing tandem runs at low populations, and transports if they sense that a quorum of nestmates is present.

In apparent support of the distance hypothesis, we found that a colony that led many tandem runs during an emigration 60 cm long (Fig. 3A), led none at all for an emigration only 10 cm long (Fig. 3B). However, closer examination reveals that the population hypothesis can also explain this result. Because scouts more readily discover a nearby site, its population grows more rapidly

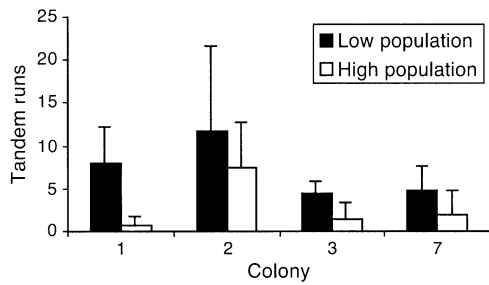


Fig. 4 Number of forward tandem runs during emigrations in which scouts found a largely empty nest (*Low population*), or a nest that had been primed with 15 ants (*High population*). A 2-way ANOVA found a significant effect of treatment on number of tandem runs ($F=12.0$, $P=0.0020$, $n=32$), but no effect of colony ($F=2.3$, $P=0.11$, $n=32$). Data were log-transformed to achieve normality and equality of variances

than that of a distant one (compare population curves in Fig. 3A and B). Hence ants at a nearby site may fail to lead tandem runs simply because a quorum is already present by the time they begin to recruit.

The Initiation experiment provided more decisive evidence against distance, and in favor of population. In the Low treatment, when the number of scouts allowed to discover a site only 10 cm from the old nest was sharply limited, the early tandem-run phase typical of longer emigrations was restored (Fig. 3C). One explanation of this result is that the obstacles imposed to restrict discovery rate themselves induced tandem runs, by making discovery slow and difficult. This explanation is rejected by the behavior of colonies in the High treatment, where discoverers faced similar restrictions but encountered nests whose populations had been primed at the start of the emigration. In this treatment, the tandem-running phase was reduced or completely eliminated (Fig. 3D), with the mean number of tandem runs significantly lower than in the Low treatment (Fig. 4).

Maintenance of tandem running

The results of the Maintenance experiment indicate that the continuation of tandem running depends on the number of ants in the new nest. Ants that were prevented from bringing their recruits into the new site led significantly more tandem runs (8.0 ± 5.5 , $n=8$) than control ants from the Low treatment of the Initiation experiment (2.9 ± 1.8 , $n=24$) (Mann-Whitney: $P=0.017$). The increase was often quite striking, with as many as 16 tandem runs led over nearly 4 h, a far greater effort than the 6 tandem runs over 1.8 h led by the most persistent control ant.

Frustrated recruiters also refrained from switching to transport for a significantly longer period (165.3 ± 74.8 min, $n=8$) than control ants (48.2 ± 30.9 min, $n=24$) (Mann-Whitney: $P=0.001$), although the details varied among the 8 experimental ants. Two started transport only when additional discoverers were allowed to enter the new nest. Two others led only a few tandem runs, and then

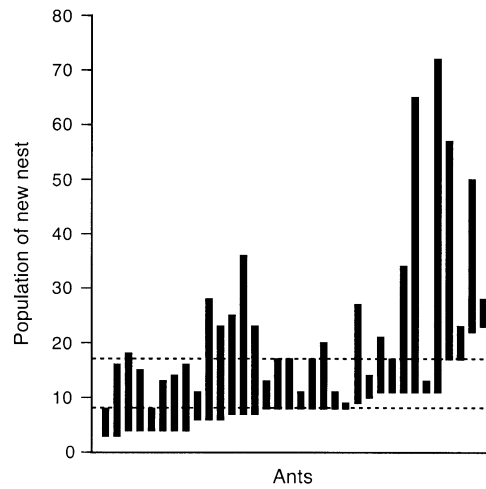


Fig. 5 Estimate of nest site population at which ants switch from tandem running to transport. The ends of each *black bar* show the upper and lower bounds of the estimate for a single recruiter. The *dotted lines* show the median upper and lower bounds, respectively

ceased recruiting altogether. These ants spent much of their time wandering through the arena, as though searching for other sites. Finally, four ants eventually switched to transport even though the site was still empty.

Size of transport quorum

To estimate the population size at which tandem runs give way to transport, we returned to the 12 unmanipulated emigrations. As a lower bound, we measured the nest population during each tandem-run leader's last stay in the new nest before leading her last forward tandem run. Because nest population steadily increased during each emigration, this gave the largest population at which the ant still decided to lead tandem runs. As an upper bound, we took the population during the same ant's last stay in the new nest before her first transport. This gave the lowest population at which she elected to perform a transport. These bounds varied widely among recruiters (Fig. 5), but their median values enclosed a region between 9 and 17 ants. Linear regression showed a small but significant effect of worker population on both the low ($\beta=0.06$, $r^2=0.12$, $n=34$, $P=0.024$) and the high ($\beta=0.22$, $r^2=0.20$, $n=34$, $P=0.004$) estimates of quorum size.

Model of quorum effect on decision-making

We derived the above results from emigrations in which only one new nest site was available. We suspected, however, that the ants' recruitment strategy may also help colonies to minimize splitting when they choose among several sites. Earlier work has shown that the colony's choice emerges in part from quality-dependent delays in the initiation of recruitment (Mallon et al. 2001).

We hypothesized that the quorum requirement demonstrated here could amplify this effect, because better nests will more readily achieve a quorum, and thus sooner enjoy accelerated recruitment via transport.

To explore the plausibility of this scenario, we developed a model based on our empirical description of recruitment behavior. The model assumes a colony whose old nest has become unsuitable, and M sites of varying quality for them to choose among. The colony has a total population, including brood items, of N members. A proportion p of these are active ants who find, evaluate, and recruit to potential new homes. All other colony members must be transported to the chosen site. Each active ant can be in one of three classes: searching for new sites (S), assessing a site i she has discovered or been recruited to (A_i), and recruiting to a site she has finished assessing (R_i). The numbers of ants in each class change over time according to the following equations:

$$\frac{dS}{dt} = - \sum_{j=1}^M \mu_j S - \sum_{j=1}^M \lambda_j I(R_j, S) \quad (1)$$

$$\frac{dA_i}{dt} = \mu_i S + \lambda_i I(R_i, S) + \sum_{j \neq i} (\rho_{ji} A_j - \rho_{ij} A_i) - k_i A_i \quad (2)$$

$$\frac{dR_i}{dt} = k_i A_i + \sum_{j \neq i} (\rho_{ji} R_j - \rho_{ij} R_i) \quad (3)$$

Searchers discover site i at per capita rate μ_i . They may also be led to a site by recruiters working at per capita rate λ_i . However, active ants are only recruited to site i if R_i is below the threshold T at which recruitment switches from tandem runs to transports. This switching rule is represented by the function I :

$$I(R_i, S) = \begin{cases} R_i, & \text{if } R_i < T \text{ and } S > 0 \\ 0, & \text{otherwise} \end{cases} \quad (4)$$

Assessors in turn become recruiters at per capita rate k_i . Because k_i is directly related to site quality, ants spend less time assessing better nests before beginning to recruit to them. Finally, assessors and recruiters at site j encounter site i and switch their allegiance to it at per capita rate ρ_{ji} . This term accounts for the previously reported ability of ants to compare sites and choose the better one, if they encounter one nest while assessing or recruiting to another (Mallon et al. 2001).

The population P_i of passive ants and brood items at site i changes according to:

$$\frac{dP_i}{dt} = \phi_i J(R_i, P_0) \quad (5)$$

where ϕ gives the per capita rate of transport. The function J confines transport to sites with at least T recruiters:

$$J(R_i, P_0) = \begin{cases} 0, & \text{if } R_i < T \text{ or } P_0 = 0 \\ R_i, & \text{otherwise} \end{cases} \quad (6)$$

P_0 gives the number of passive items remaining in the old nest.

We solved the model for a situation that mirrors the experiments of Mallon et al. (2001), in which colonies

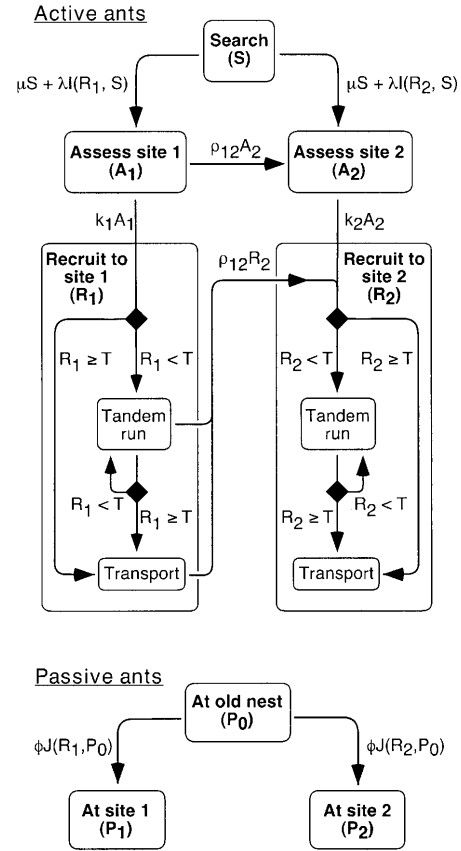


Fig. 6 Recruitment decision model, for a colony choosing between an inferior site 1 and a superior site 2

choose between two alternative sites, with site 2 superior to site 1 (Fig. 6). The sites are equidistant from the old nest, so that each is discovered at the same rate μ , and recruited to at the same rates λ and ϕ . We also assume that switching occurs only from the worse to the better site (i.e., $\rho_{21}=0$). This is based on the finding that ants encountering two sites of different quality almost invariably recruit only to the better one (Mallon et al. 2001). We solved the model numerically for a range of values of the quorum size T . Other parameters were estimated from the data reported here and in Mallon et al. (2001) (Table 1). Runs were compared on the basis of time until all colony members had been brought to site 2. If the run ended in a split between sites, we modeled an additional emigration phase in which items at site 1 were brought to site 2, at per capita rate c .

The results show a clear effect of quorum size on time to completion (Fig. 7A). A broad middle zone ($T \approx 8-30$) offers the speediest emigrations, but duration increases sharply at low values, and more gradually at higher ones. If we break the emigration into periods separated by major milestones, it becomes clear that the middle zone owes its speed to site 1's failure to achieve a transport quorum. As a result, the entire colony is moved directly to site 2. At lower quorum sizes, transport begins to both sites, although it does so sooner to site 2. A minority of

Table 1 Parameter estimates for a model of an emigrating colony choosing between two nest sites, as shown in Fig. 6. Site 1 corresponds to an artificial cavity 0.8 mm in height, and site 2 to an otherwise identical cavity 1.6 mm in height. All data are from the

12 emigrations described in this paper, unless otherwise noted. Parameters were estimated independently for each emigration, and reported as the mean and standard deviation across emigrations

Parameter	Definition	Estimate	SD
N	Colony population, including brood	208	99
p	Proportion of colony population consisting of active ants ^a	0.25	0.1
λ	Rate of recruitment by tandem runs, per ant	0.033 tandem runs/min	0.016
ϕ	Rate of recruitment by transports, per ant	0.099 transports/min	0.02
μ	Rate of discovery of new sites, per ant, per site ^b	0.013 min ⁻¹	0.006
k_1	Probability per minute that an assessor at site 1 begins to recruit ^c	0.015	0.006
k_2	Probability per minute that an assessor at site 2 begins to recruit ^c	0.02	0.008
ρ_{12}	Rate of switching allegiance from site 1 to site 2, per ant ^d	0.008 min ⁻¹	0.004
c	Time to move an item from site 1 to site 2 after old nest is empty ^e	4.6 min	–

^a Includes all recruiters plus any non-recruiters that gave evidence of searching for nest sites: i.e., those that found the new nest independently or followed a tandem run.

^b Inverse of the mean interval, for each active ant, between the start of the emigration to the time when she A) discovered the new nest, B) began to follow a tandem run toward the new nest, or C) was carried to the new nest.

^c From Mallon et al. (2001).

^d Inverse of the mean interval, for each active ant, between her first arrival at a new site and her first arrival at the other site (or the end of the emigration, if she never found the other site). Data are from emigrations in which colonies chose between two equidistant sites of different quality (Mallon et al. 2001).

^e From a single emigration in which a colony took 60 min, after the old nest was empty, to move 13 items from the inferior to the superior nest (Mallon et al. 2001).

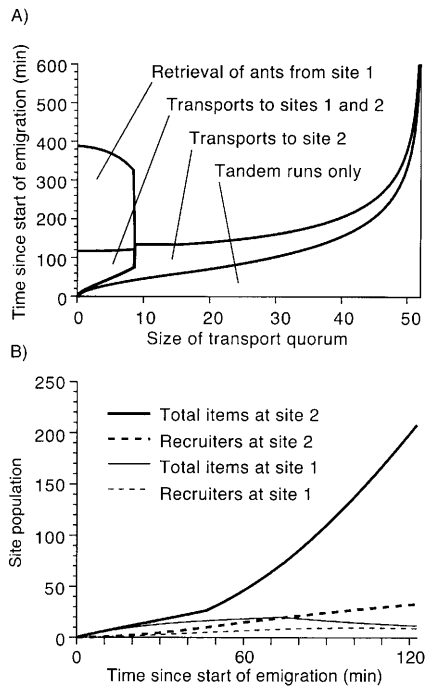


Fig. 7A, B Results of model shown in Fig. 6. **A** Time until completion of emigration, for different quorum sizes, subdivided by type and destination of recruitment behavior. **B** Time course of population growth at alternative nest sites, for a quorum size of ten ants

the colony is thus carried to site 1 and must be retrieved in a lengthy reunification phase. At higher quorum sizes, the better site maintains its advantage, but emigration time increases, because colonies must spend longer in the slow tandem-run phase before initiating rapid transport.

Figure 7B shows in greater detail how a moderate quorum size can prevent colony division. It depicts the

time course of a single emigration at a quorum size of 10. The total number of ants at each site first grows quite slowly, because recruiters use only tandem runs. Site 2, however, enjoys somewhat faster growth, because of its higher rate of recruitment initiation ($k_2 > k_1$). This allows site 2 to achieve a quorum early and thus to widen its lead markedly by switching to transport. Site 1 never achieves a quorum, and eventually begins to lose recruiters and assessors, as these ants gradually encounter the better site and switch their allegiance.

Discussion

Individual rules and collective decisions

When an emigrating colony of *Leptothorax albipennis* chooses among nest sites, the separate decisions of many workers must somehow be integrated into a single, colony-wide choice. This integration is achieved in part through direct comparisons made by workers who visit more than one site, compare them, and recruit only to the best one (Mallon et al. 2001). These comparisons cannot, however, fully explain the colony's decision-making abilities. Even in simplified laboratory conditions, with only two nearby sites to choose between, half the recruiters visit only one site (Mallon et al. 2001). Moreover, regardless of the number of sites she knows about, no worker moves more than a fraction of the colony's population. The colony's success therefore requires that each worker coordinate her limited knowledge and activity with that of her nestmates. Our results, combined with those of Mallon et al. (2001), suggest that ants accomplish this by drawing on two sources of information: (1) their own independent assessment of a site that they have inspected; and (2) their attention to a cue – site population – that indirectly informs them of the assessments of their nestmates.

The heart of a worker's decision strategy is her incremental acceptance of a potential site. She first condenses a host of features, including floor area, entrance size, cavity thickness, and light level, into a single measure: an instantaneous probability of starting to recruit (Mallon and Franks 2000; Mallon et al. 2001; E.B. Mallon and N.R. Franks, personal communication). The better the nest, the higher this probability, and thus the shorter the latency until recruitment begins. At this point, the ant's acceptance is provisional, and she confines herself to summoning other active ants via tandem runs. Full acceptance comes only when the site's population meets the transport quorum, and the ant both accelerates her recruitment and changes its target to passive nestmates.

This two-stage decision process offers several advantages for efficient emigration and accurate decision-making. Most obviously, waiting for a quorum ensures enough recruiters for efficient transport of the rest of the colony. More interestingly, the quorum requirement allows each ant to check her provisional acceptance against the independent judgements of her nestmates. Because several variables must be weighed and integrated, site assessment may be prone to errors. If such errors lead an ant to recruit prematurely to a relatively poor site, her followers will likely counter her mistake by judging the site more harshly than she, delaying recruitment for longer, and thus putting off the start of transport.

The greatest advantage of the ants' decision rules may be in improving the efficiency with which colonies move into the best available nest. The model presented above shows this effect clearly in the large time penalty paid by colonies using a quorum size of zero (Fig. 7A); that is, colonies are more likely to split if the ants launch immediately into transport, without taking into account the behavior of their nestmates. The quorum requirement reduces the chance of splitting, by creating a competition among nest sites for a limited resource – the pool of active ants. Better nests will tend to win this competition, due to their shorter recruitment latencies. Thus only the best will experience the accelerated recruitment of the transport phase.

It is not known whether other social insects similarly rely on a quorum of workers to arrive at a collective decision. Emigration by the ant *Myrmica rubra* is an appealing candidate, since it also relies on two recruitment methods in distinct phases (Abraham and Pasteels 1980). More generally, there are many cases in which workers integrate limited direct information with cues from nestmate interaction. A foraging honey bee, for example, decides whether and how vigorously to recruit to a food source on the basis of her independent assessment of its quality, but she modulates this decision on the basis of the delay she experiences finding a house bee to receive her nectar (Seeley 1995). This behavior underlies the colony's ability to choose the better of two food sources in the absence of direct comparisons by individual bees. Many ant species similarly combine independent assessment of food sources with indirect communication

through odor trails, to make adaptive colony-level foraging choices (Beckers et al. 1990; deBiseau et al. 1991).

Mechanisms of this kind are not restricted to social insects. Many bacteria regulate density-dependent behavior by means of quorum sensing, in which the relevant behavior is released only when the concentration of a signal molecule produced by each bacterium reaches a threshold (Miller and Bassler 2001). In an even stronger parallel from immunology, a recent model has shown how a T-cell's decision to mount a response against a given antigen can emerge from cooperative interactions among thousands of cell-surface receptors (Chan et al. 2001). Under this model, individual receptors become activated on the basis of purely local binding with ligand, but, like *Leptothorax* scouts, they go through a preliminary stage of partial activation before responding fully. Also like the ants, receptors proceed more rapidly through these stages for "better" ligands: i.e., those most similar to the antigen the cell has been selected to detect. Moreover, their passage from one stage to another depends both on their independent binding of ligands, and on interactions with neighboring receptors that can enhance or reduce their responsiveness. The model shows that this cooperation can significantly improve the specificity with which a cell can detect foreign antigens.

Reverse tandem runs

The idea that switching to transport marks full commitment to a nest site may partly explain the puzzling reverse tandem runs seen during the transport phase. The ants' recruitment decisions can be neatly summarized around the organizing principle of a "home nest". We hypothesize that each active ant has a single place that she designates as home, that she leads tandem runs *away* from home to a place where assistance is required, and that she performs transports *toward* home to retrieve lost or misplaced nestmates. At first the old nest, although damaged, is still everyone's home. Thus, if a scout encounters a lost ant in the arena, she transports her to the old nest. Likewise, she leads tandem runs away from the old nest to summon help in evaluating a promising site. Only if the site's population achieves a quorum does it become the ant's home, and thus the destination of all her transports, as well as the origin of all her tandem runs.

If this scenario is correct, then what task are reverse-tandem followers being summoned to perform? A simple possibility is that reverse-tandem leaders want their followers to consider moving the colony back to the old nest, perhaps because crowding and disorder at the new site has reduced its attractiveness. Rosengren (1971) hypothesized a similar explanation for two-way carrying behavior between nest sites in wood ants. This scenario, however, does not seem likely for *L. albipennis*, because reverse runs usually ended with the leader immediately carrying an item from the old to the new nest, clearly showing her continued commitment to the new site. A

second possibility is that reverse runs stimulate transport by idle workers already at the new nest. At best this can be only a partial explanation, given that half of reverse-run followers were already transporting from the old nest, so that recruitment only mired them in slow tandem runs and so retarded their retrieval efforts.

A more promising possibility, although still speculative, is that reverse runs serve not to stimulate recruitment but to re-allocate it. Such re-allocation could be useful, if the items to be retrieved were not concentrated at the old nest, but instead were spread among several sites to which other ants had moved them. In nature, such temporary splitting may be quite common, if more than one site reaches the transport threshold. Ants and brood will then be carried to several sites and must later be brought to the single best one. The quality-dependent recruitment latencies and quorum requirement described here and in Mallon et al. (2001) can reduce the likelihood of such splitting, but they probably cannot prevent it altogether. Thus emigration may be a dynamic and drawn-out process, with ants and brood percolating through a network of sites before coalescing onto the best one. In such a system, reverse-tandem runs could be a useful tool for redirecting transport effort from one branch of the network to another.

Why two recruitment methods?

Speedier transports at first seem the best method for recruiting both passive and active ants, given the likely benefit of rapidly completing the emigration and ending the colony's exposure. Tandem runs, however, may better allow recruits to learn the route between the nests, so that they can later follow it independently. Because a tandem follower adopts the same posture that she will use when travelling on her own, she can better learn visual cues known to guide navigation in these ants (Pratt et al. 2001; McLeman et al. 2002). Walking also allows her to deposit orientation pheromones, another possible guidance cue (Maschwitz et al. 1986; Aron et al. 1988; Mallon and Franks 2000). In contrast, a passively transported ant cannot lay trails, and the posture in which the ants are carried, with their heads upside down and pointing backwards, is not well suited to learning visual cues.

Quorum detection and variability

Ants need not actually count nestmates to determine whether the quorum has been reached, but could instead monitor an accessible cue that is correlated with population. For example, an ant could measure the time interval between her arrival at the site and her first encounter with a nestmate, or the mean interval between encounters over the course of her visit. Both of these are likely to be negatively correlated with population. Similar abilities to respond to time intervals or encounter rates are well known in other social insects (Seeley 1989, 1992;

Anderson and Ratnieks 1999; Gordon and Mehdiabadi 1999; Jeanne 1999).

The ants' method of quorum detection may contribute to the marked variation in population size at which each ant switched to transport (Fig. 5). Stochastic variation in encounter rates, for example, could cause two ants simultaneously visiting a site to arrive at different estimates of its population. However, some variation may instead reflect functional differences in quorum size. A correlation between quorum size and colony population, for example, could help colonies to match the timing of their initiation of transport to the ease with which they can summon a corps of active ants to a nest site. Thus large colonies could avoid a premature decision and small colonies a tardy one. Consistent with this idea, we found a weak but significant effect of population size on estimated quorum size. More rigorous experiments are still required to determine whether this is a true causal relationship, or simply a reflection of the speedier increase in nest population possible in large colonies.

Because we manipulated only the population of adult workers, we cannot say whether brood items also contribute to the quorum. In any event, workers are likely to be more important, because no brood items are recruited during the tandem-run phase, and thus only workers will contribute to the end of this phase and the start of transport. For those ants that start to recruit only later in the emigration, however, brood items could serve as a clear sign that the transport phase has begun.

Influence of time on switch to transport

Other factors beside nest population probably influence an ant's choice of recruitment method. In the Maintenance experiment, some ants eventually switched to transport, even though the new site remained empty. Interestingly, the switch always followed a tandem-run phase much longer than that of control ants. This implies that a recruiter may commit to a site in the absence of nestmates, if enough time has elapsed since she began leading tandem runs. In nature, such a rule could prevent stalemates when too many sites are discovered, so that no single site can attract a quorum.

Simple ants versus local information

Decentralized information processing by insect societies is often characterized in terms of cognitively simple individuals cooperating to accomplish sophisticated colony-level tasks (Beckers et al. 1990; Detrain et al. 1999). While there can be no doubt of the complexity of the colony's achievements, the assumed simplicity of individuals is less convincing. *Leptothorax* workers have impressive information-processing skills, as displayed in their assessment and integration of several features of nest design, and their ability to compare the quality of two sites and reliably choose the better one (Mallon et al.

2001). Moreover, as shown in this paper, they use two different kinds of recruitment behavior and an elegant context-dependent rule for switching between them.

The collective achievements of these colonies draw attention, not to a gap between the intelligence of workers and the colony as a whole, but rather to the difference in scale. Even when no insect possesses information on more than a small part of the colony's task, an adaptive global solution can emerge from their local interactions, guided by appropriate individual behavioral rules. Because these local interactions may themselves involve sophisticated information processing, a thorough understanding of colony cognition requires a full appreciation of the cognitive skills of individual insects.

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