



An agent-based model of collective nest choice by the ant *Temnothorax albipennis*

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Colonies of the ant *Temnothorax* (formerly *Leptothorax*) *albipennis* can collectively choose the best of several nest sites, even when many of the active ants who organize the move visit only one site. Previous studies have suggested that this ability stems from the ants' strategy of graded commitment to a potential home. On finding a site, an ant proceeds from independent assessment, to recruiting fellow active ants via slow tandem runs, to bringing the passive bulk of the colony via rapid transports. Assessment duration varies inversely with site quality, and the switch from tandem runs to transports requires that a quorum of ants first be summoned to the site. These rules may generate a collective decision, by creating and amplifying differential population growth rates among sites. We test the importance of these and other known behavioural rules by incorporating them into an agent-based model. All parameters governing individual behaviour were estimated from videotaped emigrations of individually marked ants given a single nest option of either good or mediocre quality. The time course of simulated emigrations and the distribution of behaviour across ants largely matched these observations, except for the speed with which the final transport phase was completed, and the overall emigration speed of one particularly large colony. The model also predicted the prevalence of splitting between sites when colonies had to choose between two sites of different quality, although it correctly predicted the degree of splitting in only four of six cases. It did not fully capture variance in colony performance, but it did predict the emergence of variation in individual behaviour, despite the use of identical parameter values for all ants. The model shows how, with adequate empirical data, the algorithmic form of a collective decision-making mechanism can be captured.

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Group living expands the behavioural complexity of animals, by making possible collective acts that arise from interactions among group members. Examples range from simple aggregation (Deneubourg et al. 1990, 2002) to highly coordinated group movements (Couzin & Krause 2003), synchronized signalling (Greenfield 1994), and cooperative group hunts (Heinsohn & Packer 1995; Boesch 2002). Some of the most elaborate cases are found in the social insects, where the primacy of colony success in determining individual fitness has freed natural selection to mould exceptionally intricate collective phenotypes (Seeley 1995; Camazine et al. 2001). These orderly global patterns emerge without central control by well-informed leaders, each animal instead applying appropriate decision

rules to purely local information. Understanding this emergence is hindered by the number and variety of group members, and the nonlinearity and stochasticity of their interactions. Because intuition alone can rarely take in this complexity, understanding can better advance through development of mathematical models. Agent-based models are a particularly powerful tool for dissecting collective mechanisms (Tofts 1991; de Vries & Biesmeijer 1998; Sumpter et al. 2001). By distilling the behavioural rules followed by group members (or agents) into a computer algorithm, these models can use simulation and mathematical analysis to predict the collective properties of the group. Comparison of predicted and observed behaviour can then test the adequacy of hypothesized local rules and interactions to generate known global phenomena.

Despite their natural applicability to insect societies, agent-based models have seldom been usefully applied. Their main weakness has been the lack of adequate data to reliably estimate model parameters. As a result of

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Seeley's (1995) extensive experimental investigations using individually marked bees, the most thoroughly developed models are of honeybee foraging (Seeley et al. 1991; de Vries & Biesmeijer 1998; de Vries & Biesmeijer 2002). Even here, parameters have been estimated under a variety of experimental conditions, with little control for environmental and between-colony variation. As a result, these models have limited power to make general predictions.

In this paper we develop an agent-based model of collective nest site choice by the ant *Temnothorax* (formerly *Leptothorax*) *albipennis*. To estimate the model's parameter values, we use extensive data on hundreds of individual ants in several colonies over multiple emigrations. We achieve this by taking advantage of this species' small colony size, allowing every ant to be individually marked, and the readiness of colonies to emigrate in controlled laboratory conditions, where extensive videotaped records of their behaviour can be made. We focus on emigration behaviour likely to be of importance in the ants' natural setting, where they inhabit small, preformed cavities whose fragility may compel frequent moves. In the laboratory, a colony whose nest has been damaged not only efficiently moves to a new site within a few hours, but also reliably chooses the best site from as many as five alternatives, discriminating among sites according to cavity area and height, entrance size and light level (Mallon & Franks 2000; Mallon et al. 2001; Pratt & Pierce 2001; Franks et al. 2003b).

Previous studies have yielded a detailed description of the worker behaviour underlying a colony's abilities (Mallon et al. 2001; Franks et al. 2002; Pratt et al. 2002). Emigrations are organized by a subset of active workers, about one-third of the population, who search for potential new homes, assess their quality, and recruit nestmates to promising finds. These ants follow a strategy of graded commitment to a site they have found, with transitions to higher levels depending both on site quality and on interactions with nestmates. At the lowest level of commitment, an ant repeatedly visits a site but does not recruit to it. She remains at this level for a duration inversely related to the site's quality. At the next level, she confines herself to recruiting other active ants via tandem runs, in which a single follower is slowly led from the old nest to the new site. The new arrivals themselves make independent decisions about whether to recruit to the site. An ant enters the highest level of commitment according to a quorum rule: once a threshold of ants is present at the new site, she replaces tandem runs with transports, in which a nestmate is simply picked up and carried to the new site. This switch marks not only an acceleration of recruitment, transports being three times faster than tandem runs, but also a change in its target, from active movers to brood items and passive adults.

This strategy of graded commitment may be a key component of the colony's decision-making abilities. The quality-dependent difference in assessment duration ensures faster population growth at better nests. The quorum rule amplifies this difference and acts as a check on individual decisions, ensuring full commitment only to nests good enough to attract the continued attention of

several ants. Thus, if a colony simultaneously considers two sites of different quality, the better one should reach the transport quorum sooner and experience accelerated population growth. Ideally, the entire colony will be moved to the better site before the worse one achieves a quorum. Even if some ants are transported to the worse nest, a differential equation model has suggested that the graded strategy will reduce the incidence of colony splitting (Pratt et al. 2002).

Can this scheme really account for a colony's decision-making abilities? To answer this question, we must consider not only the collective result of many interacting ants following these recruitment rules, but also other potentially important features of the ants' behaviour. For example, ants that encounter two sites of different quality will subsequently confine their recruitment to the better one (Mallon et al. 2001). Although many, if not most, ants never visit more than one site, even a few such comparisons might have important effects at the colony level. Also, transporting ants occasionally lead 'reverse' tandem runs from the new site to the old (Pratt et al. 2002). The function of these runs remains unclear, with possibilities including the enhancement of recruitment effort, its redirection from one site to another, or the guidance of poor navigators by good ones. These effects could be important if the colony splits and must later coalesce at a single site. Finally, although most transports are of passive ants, active ants may also be transported, usually after being picked up while searching the arena (Pratt et al. 2002).

The agent-based model of emigration we present here incorporates everything learned to date about the behaviour of individual ants. The goals are to test the adequacy of this behaviour to explain colony-level performance, and to create a tool for deeper analysis of a colony's collective decision-making abilities. We first describe the form of the model, specifying the behavioural states open to the ants and the parameters governing transitions among them. We then estimate parameter values from experimentally induced emigrations in which the ants are offered a single new nest site. To test the model, we use it to simulate these same emigrations and compare a suite of statistics measured from real and simulated colonies. We further test the model by comparing its predictions to an independent set of emigrations in which colonies are required to choose between two sites of different quality.

METHODS

Structure of the Model

We model a colony's selection of a new nest after its current home has been destroyed. Each of the active ants responsible for organizing the emigration is represented as a distinct agent, and its behaviour modelled as a network of states connected by transition probabilities (Fig. 1). Although this network contains many states, its fundamental structure is quite simple. All states belong to one of four major phases of decision making, indicated by colour in Fig. 1. Each ant begins in the Exploration phase (blue), during which she searches for potential new homes. The

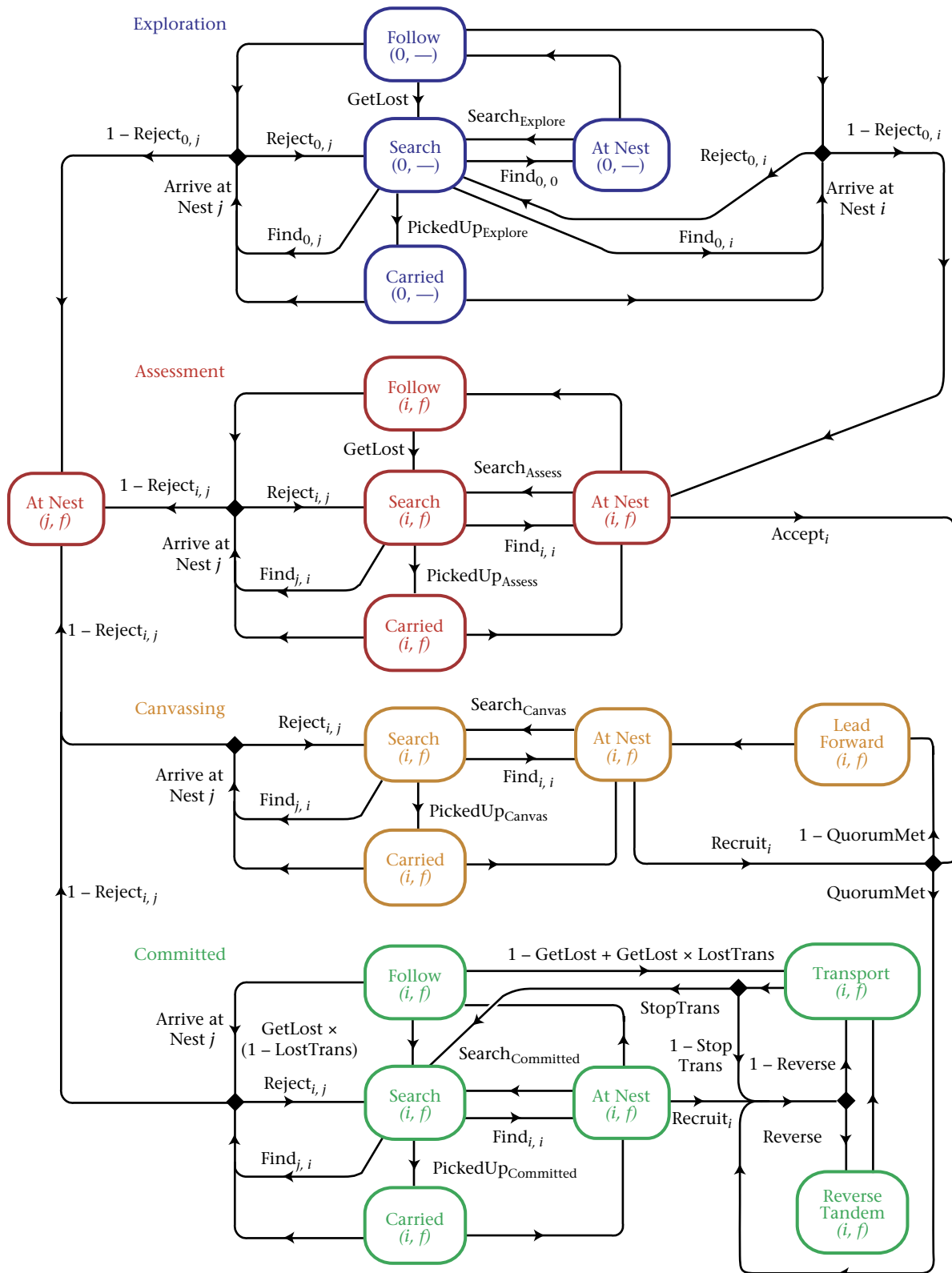


Figure 1. Model of the behaviour of active ants responsible for organizing colony emigrations. Boxes represent behavioural states and arrows represent transitions between them. Colours indicate the four major levels of an ant's commitment to a candidate nest site: Exploration (blue), Assessment (red), Canvassing (amber) and Commitment (green). The first subscript i in each state identifies the nest that the ant is currently assessing or recruiting to. The second subscript f identifies the nest from which the ant recruits (either the old nest or a rejected new site to which nestmates have been brought by other ants).

next three phases follow once she finds a site, each phase representing an increased degree of commitment to that site. In the Assessment phase (red), the ant evaluates the site but does not recruit to it. In the Canvassing phase (amber), she provisionally accepts the site and leads tandem runs of other active ants who then make their own assessments. Finally, in the Committed phase (green), the ant makes a complete commitment to the site, rapidly transporting passive adults and brood items.

The states and transitions within each major phase detail how the ant encounters new sites and communicates their locations to nestmates. Each ant begins the emigration in the Exploration phase at the old nest, 0 (state At Nest), from which she can take one of three routes to arrive at a new site i . First, she can leave the nest to search (Search), at rate $\text{Search}_{\text{Explore}}$, and then independently discover i at rate $\text{Find}_{0,i}$. Second, she can follow a tandem run to i (Follow). Third, she can encounter a committed ant while searching and be carried by her to i (Carried). These routes intersect with each other, because followers become searchers if they lose contact with their tandem leader before reaching the goal (at rate GetLost), and because searching ants periodically return to the old nest (at rate $\text{Find}_{0,0}$), where they again become available to follow tandem runs. Once an ant arrives at site i , she may reject it and continue searching, with a probability ($\text{Reject}_{0,i}$) that depends on the site's quality relative to the old nest. Otherwise, (with probability $1 - \text{Reject}_{0,i}$), she enters the Assessment phase at i .

In the Assessment phase the ant alternates between stays inside site i , during which she evaluates it as a potential new home, and searches in the surrounding area (initiated at rate $\text{Search}_{\text{Assess}}$). During these searches she may encounter other new sites j , via the same three routes as exploring ants, or she may return to the current site i (at rate $\text{Find}_{i,i}$). She may also be picked up while searching and carried back to i . While in state At Nest, she may provisionally accept the site, at rate Accept_i , an increasing function of nest quality. If so, she enters either the Committed phase (with probability QuorumMet, an increasing function of site population) or the Canvassing phase (with probability $1 - \text{QuorumMet}$).

On becoming a canvasser, the ant leaves the new site and attempts to lead a tandem run to it from the old nest (Lead Forward). This attempt may fail, if she finds no followers at the old nest or if she loses her follower on the way. Successful or not, the attempt ends with her back in the new site (At Nest). She then leaves the site either to recruit again (at rate Recruit_i), or to search the surrounding area (at rate $\text{Search}_{\text{Canvas}}$). If she searches, she may encounter other new sites, either by being carried to them or by independently discovering them, or she may return to site i (at rate $\text{Find}_{i,i}$) or be carried back to it. If she recruits, she first re-evaluates the site's population, and either leads another tandem run (with probability $1 - \text{QuorumMet}$), or moves on to the Committed phase (with probability QuorumMet).

On entering the Committed phase, either directly from Assessment or via Canvassing, the ant returns to the old nest to transport a nestmate. On the journey to the old nest, she may attempt to lead a reverse tandem run (with

probability Reverse). At completion of the transport, either she transports again (with probability $1 - \text{PauseTrans}$) or she searches the surrounding area (with probability PauseTrans). While searching, she may encounter other new sites or return to site i , as in the earlier phases. Once back in the site after a search, the ant may follow one of three paths. First, she may leave again to search (at rate $\text{Search}_{\text{Committed}}$). Second, she may follow a tandem run to an alternative new site or back to the old nest (Follow). Third, she may return to the old nest and transport a nestmate (at rate Recruit_i).

When an ant in any phase encounters a new site j , she may reject it and carry on searching, with probability $\text{Reject}_{i,j}$ dependent on the site's quality relative to her current site i . If she does not reject it, then she becomes an assessor of the new site.

The transition probabilities and decision rules used by an ant often depend on which nests she has already visited. This will determine, for example, the origin and destination of her tandem runs and transports, and her probability of rejecting a new site she has found. Thus, each behavioural state has two subscripts indicating (1) the site that the ant is currently assessing or recruiting to (denoted by i), and (2) another site of which the ant has knowledge and to which she returns to find recruits (denoted by f). During the Exploration phase, f has no value until the ant finds a new nest, at which time it is set to zero (denoting the old nest).

Experimental Emigrations

Two sets of emigrations were observed. The first generated estimates of parameter values, as well as data for comparison to the model's predictions. To aid observation of individual behaviour, each of the workers in these colonies received distinctive combinations of paint marks on the head, thorax and gaster. A second set of emigrations allowed an additional, independent test of the model. Because these tests focused on predictions of colony-level behaviour, these ants were not individually tracked.

Data for parameter estimation

Parameter values were estimated from laboratory observations of 12 emigrations by six queenright colonies. Each colony was induced to emigrate once to a good and once to a mediocre nest. Each nest consisted of a cardboard perimeter sandwiched between two large microscope slides (50×76 mm). A small entrance was cut through one wall of the perimeter. The two nest types had identical entrance widths (2 mm) and cavity floor dimensions (25×33 mm), but the better nest had a thicker cavity (1.6 mm) than did the mediocre one (0.8 mm). Previous studies have shown a significant preference for the thicker cavity (Mallon et al. 2001; Franks et al. 2003b). Emigrations were observed in a large Plexiglas tray ($75 \times 43 \times 7$ cm), the walls of which were coated with Fluon to prevent the ants' escape. Old and new nests were separated by 65 cm.

Emigrations were induced by removing the upper slide from the old nest, causing the exposed ants to seek a new

home. The interior of the new nest was videotaped throughout the emigration. In the two emigrations by colony 6, the old nest was also videotaped. The start and end times and the participants of tandem runs that occurred out of camera range were noted by an observer. Further details on these emigrations are reported in Mallon et al. (2001) and Pratt et al. (2002).

During playback of the videotapes, we recorded (1) the time of every entry and exit at the new 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 estimated parameter values from this raw data, as described in detail below, using the statistical analysis package R (Venables & Ripley 2002).

Data for model validation

The model was validated by comparison to emigrations by six queenright colonies choosing between two nests of different quality. Colonies were not the same as those that provided parameter estimates. Nests were constructed of balsa wood slats sandwiched between large glass slides (50 × 76 mm), with a 1.6-mm diameter entrance hole drilled through the centre of one slide. Both nest types had cavity dimensions of 17 × 23 × 1.6 mm, but the better nest was darkened with a thin sheet of neutral density filter (Rosco Cinegel no. 3404), attached with clear adhesive tape to the upper surface of the roof. Previous work has shown that the ants rank darkness especially highly when choosing between sites (Franks et al. 2003b). Emigrations were carried out as described above, but in a slightly larger arena strewn with dark wooden blocks serving as visual landmarks to aid the ants’ navigation (Pratt et al. 2001; McLeman et al. 2002). The two new sites were placed 65 cm from the old nest and 28 cm from one another.

Colony performance was assayed by measuring the degree to which the colony split between the new sites. This was taken as the ratio of brood items in the dark nest to the total number in both nests, counted from digital photographs of each site made once the old nest was empty.

Because the nest designs used in these experiments differed from those in the single-nest emigrations, new data were required to estimate $Accept_i$ and $Recruit_i$, parameters that depend on nest quality. Colony A6 was therefore induced to emigrate two additional times, once to a light and once to a dark nest. Methods were similar to those of the two-nest emigrations, except that all ants were individually marked, and the interior of the new nest was videotaped. The values of $Accept_i$ and $Recruit_i$ for each nest type were estimated from these observations, as described below.

Parameter Estimation

Parameter values, summarized in Tables 1 and 2, were based on a total of 12 896 acts by approximately 290 ants in six colonies. Below are given the definitions of each

Table 1. Parameter estimates for the agent-based model and sample sizes (N) on which they were based

Parameter	Estimate ± SE	N
Find _{0,nr} Find _{m,n}	0.01 ± 0.002/min	484
Find _{0,0}	0.18 ± 0.01/min	484
Find _{n,n}	0.09 ± 0.002/min	2028
Search _{Explore}	0.51 ± 0.02/min	473
Search _{Assess}	0.23 ± 0.01/min	1464
Search _{Canvas}	0.14 ± 0.02/min	158
Search _{Committed}	0.06 ± 0.01/min	642
PropLost	0.91 ± 0.04	55
Duration _{Forward}	7.2 ± 1.6 min	4
Duration _{Reverse}	4.6 ± 0.5 min	9
Reject _{Thick, Thin}	1.0 ± 0.0	16
Reject _{Thin, Thick}	0.03 ± 0.03	37
PickedUp _{Explore}	0.010 ± 0.001/min	110
PickedUp _{Assess}	0.005 ± 0.001/min	75
PickedUp _{Canvas}	0.005 ± 0.002/min	4
PickedUp _{Committed}	0.005 ± 0.001/min	45
Accept _{Thick}	0.053 ± 0.004/min	257
Accept _{Thin}	0.034 ± 0.006/min	278
Accept _{Dark}	0.032 ± 0.005/min	84
Accept _{Light}	0.013 ± 0.006/min	70
MinAccept	5 min	535
RecTime _{Tandem}		
Mean	b: 17 ± 1 min, a: 11 ± 1 min, k: 2.0 ± 0.9	152
SD	b: 11 ± 2 min, a: 10 ± 2 min, k: 1.5 ± 1.1	152
RecTime _{Transport}		
Mean	b: 11 ± 1 min, a: 7 ± 1 min, k: 1.5 ± 0.5	1932
SD	b: 9 ± 1 min, a: 7 ± 1 min, k: 0.6 ± 0.3	1932
PropRec _{Transport}	0.45 ± 0.01	365
PropRec _{Tandem}	0.65 ± 0.03	16
QuorumMet	T: 0.017 ± 0.001, k: 2.0 ± 0.2	443
Recruit _{Thick}	0.23 ± 0.01/min	405
Recruit _{Dark}		
Recruit _{Thin}	0.15 ± 0.02/min	395
Recruit _{Light}		
TransInNestTime	1.0 ± 0.02 min	1926
PauseTrans	0.25 ± 0.19	535
Reverse	0.06 ± 0.01	2117
LostTrans	0.56 ± 0.12	16

See text for details.

Table 2. Populations of colonies used in single-nest emigrations to estimate parameters

Colony	Nest	Active workers	Passive workers	Total workers	Total brood	Total population
1	Thick	46	51	97	141	238
1	Thin	53	53	106	145	251
2	Thick	74	84	158	187	345
2	Thin	66	83	149	190	339
3	Thick	53	33	86	104	190
3	Thin	53	33	86	97	183
4	Thick	63	42	105	60	165
4	Thin	59	40	99	60	159
5	Thick	18	20	38	3	41
5	Thin	37	17	54	8	62
6	Thick	64	30	94	152	246
6	Thin	69	44	113	152	265
$\bar{X} \pm SD$						207 ± 94

parameter and the methods by which estimates were derived. These descriptions consistently refer to the old nest as the source of recruitments and the new nest as the destination, except for reverse tandem runs. This description is accurate for cases in which only one new nest is available. However, these parameters are assumed to apply as well in more complex situations when transports and tandem runs may instead link competing new sites.

TotalPop: total colony population estimated as the mean across emigrations of the number of individually marked ants plus the number of transports of unmarked ants and brood items (Table 2).

ActiveWorkers: number of ants active in a given emigration. An ant was counted as active if she transported a nestmate, led or followed a tandem run, or independently discovered a nest site. To this total was added one-quarter of the number of transported ants that subsequently failed to recruit (Table 2). This was based on the observation in colony 6 (for which data from the old nest were available) that 20 of 81 such ants were carried from the arena, rather than the old nest, and thus were likely to have been active searchers. To estimate the number of active workers in the two-nest emigrations, we performed a linear regression of TotalPop on ActiveWorkers for the single-nest emigrations. The estimated value of ActiveWorkers was $14.7 + 0.40 \times \text{TotalPop}$ ($R^2 = 0.77$). The predicted values are given in Table 3.

Find_{*i,j*}: rate at which an ant searching from nest *i* encounters and enters nest *j*. Separate values were calculated for three distinct contexts: (1) Find_{0,0}: return to the old nest 0 by an ant in the Exploration phase; (2) Find_{*n,n*}: return to a new site *n* by an ant in the Assessment, Canvassing, or Committed phase at *n*; (3) Find_{0,*n*} and Find_{*n,n*}: discovery of a new site *n*, when searching either from the old nest 0 or from another new site *m*. Values for Find_{0,0} and Find_{0,*n*} were derived from a 50-min period early in one of the emigrations of colony 6, for which we had complete information on every entry and exit at both the old and new nests (and thus the length and outcome of every search). Find_{0,0} was estimated by survival analysis as the rate of an exponential distribution fitted to the search durations. Searches that ended with discovery of the new nest were treated as censored data. The same data also yielded an estimate of Find_{0,*n*}, by treating as censored the returns to the old nest. Find_{*n,n*} was similarly estimated from the durations of searches by ants in the Assessment, Canvassing, or Committed phases. A search was defined as

any trip outside the new nest that did not include a recruitment act. Find_{*m,n*} was assumed to equal Find_{0,*n*}.

Search_{Phase}: rate at which an ant inside a nest leaves it to search for other sites, calculated separately for each phase. Each value was estimated as the rate of an exponential distribution fitted by survival analysis to the durations of stays inside the nest. Search_{Explore} was based only on data from colony 6, for which observations at the old nest were available. For Search_{Canvassing} and Search_{Committed}, stays ending with departures to recruit were treated as censored.

GetLost: rate at which the follower of a tandem run loses contact with her leader before reaching the destination. Given the proportion of tandem runs in which the initial follower became lost (PropLost) and the duration of an average forward tandem run (Duration_{Forward}), and assuming that the point at which a follower gets lost is independent of the time she has been following, we solve $e^{-\text{Duration}_{\text{Forward}} \times \text{GetLost}_{\text{Forward}}} = 1 - \text{PropLost}$ to obtain a value for GetLost_{Forward} of 0.33/min. Similarly, we solve $e^{-\text{Duration}_{\text{Reverse}} \times \text{GetLost}_{\text{Reverse}}} = 1 - \text{PropLost}$ to obtain a value for GetLost_{Reverse} of 0.52/min. Followers were not considered lost if they entered the site within 30 s of breaking up with the leader. Estimates were derived only from the emigrations by colony 6, for which observations were made at both old and new nests.

Reject_{*i,j*}: probability that an ant assessing or recruiting to site *i* rejects a newly discovered site *j*. The value was derived from observations of Mallon et al. (2001), on colonies choosing between two nests of different quality, as the proportion of ants that encountered both sites and that subsequently recruited to the first site. Separate estimates were made for ants finding the worse nest after the better one and vice versa.

PickedUp_{Phase}: rate at which a searching ant is transported to a new site, calculated separately for each phase. The number of transports of searching ants in a given phase was divided by the time spent searching, summed over all ants in that phase. Searches before the first transport were not included, as it was impossible for an active ant to be carried until at least one nestmate had entered the Committed phase.

Accept_{*i*}: rate at which an ant begins recruiting to the nest *i* that she is assessing. This was estimated by survival analysis as the rate of an exponential distribution fitted to the duration between each active ant's first entry into the new site and her first recruitment to it. Ants that never recruited were treated as censored data. Data for thick and thin nests were fitted separately. Durations included only time inside the new site. We subtracted 1 min from the observed durations to account for an assumed minimum duration of assessment, based on the rarity of measured durations less than 1-min long (5 out of 535 observations). Durations made negative by this adjustment were set to 0.1 min.

MinAccept: minimum latency between an ant's first entry into a site and her decision to begin recruiting to it. This latency included time spent outside the new nest, and was set to 5 min, based on the rarity of latencies that brief (28 out of 535 observations).

RecTime_{Type}: duration of a recruitment trip, from leaving the new site to returning with a recruit. Because an

Table 3. Populations of colonies used in two-nest emigrations for model validation

Colony	Total workers	Brood	Total population	Estimated active workers
A4	98	228	326	70
A6	133	111	244	59
A8	157	106	263	62
A14	109	192	301	67
A16	141	61	202	53
A17	174	173	347	73

ant's trips grew shorter as she gained experience, we modelled each trip's expected length D as a function of its position n in the ant's sequence of recruitments:

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

where b is the duration at the first recruitment and k determines how fast the duration approaches its asymptotic value $b - a$. Separate functions were fitted for the two recruitment methods (Fig. 2a, b). The standard deviation of trip duration was similarly fitted (Fig. 2c, d). Forward and reverse tandems were analysed together.

PropRec_{Type}: proportion of the round-trip recruitment time spent leading a tandem run (PropRec_{Tandem}) or carrying a nestmate (PropRec_{Transport}), rather than walking alone or finding a recruit inside the nest. Estimates were derived only from the emigrations by colony 6, for which observations were made at both old and new nests. This parameter was used to calculate each recruiter's time of arrival at the old nest. For trips including both a transport and a reverse tandem run, PropRec_{Tandem} was used.

QuorumMet: probability that a canvassing ant switches to transport upon leaving the new nest to recruit, as a function of nest population. For each independent recruitment decision, we measured the mean population of the new nest during the recruiter's immediately preceding stay in that nest. Independent decisions included

only those leading to forward tandem runs or to each ant's first transport, because the ants cease monitoring nest population once the switch to transport has been made (Pratt 2005). Mean populations were divided by the colony's total population, to account for possible scaling of the quorum with colony size. Recruitment decisions were scored as either 0 (tandem run) or 1 (transport), and their dependence on population fitted with a Hill function:

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

where S is the probability of switching to transport and P is the normalized mean nest population. T is the population at which the probability equals 0.5 and can be taken as the quorum size, and k determines the non-linearity of the response, with higher k yielding a more step-like function. The resulting fit (Fig. 3) was used in the simulations to generate the probability of switching to transport at each recruitment decision.

Recruit_i: rate at which a canvassing or committed ant leaves nest i , either to lead a tandem run or to begin a series of transports. This value was estimated separately for thick and thin nests as the rate of an exponential distribution fitted by survival analysis to the durations of stays inside the nest. Stays that ended with departures to search were treated as censored data.

PauseTrans: probability that a committed ant ends a series of transports by leaving the new nest to search,

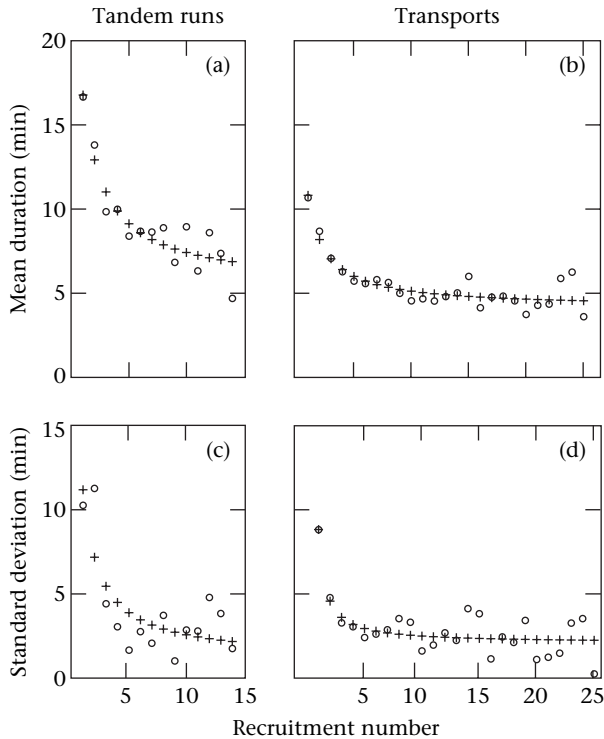


Figure 2. Estimates of the mean and standard deviation of RecTime, the duration of a round-trip recruitment journey, as a function of the number of recruitment journeys so far undertaken. Data are plotted separately for tandem runs (left panes) and transports (right panes). Circles mark the mean (top row) or standard deviation (bottom row) of journey duration for each recruitment number. Crosses mark the fits to these data.

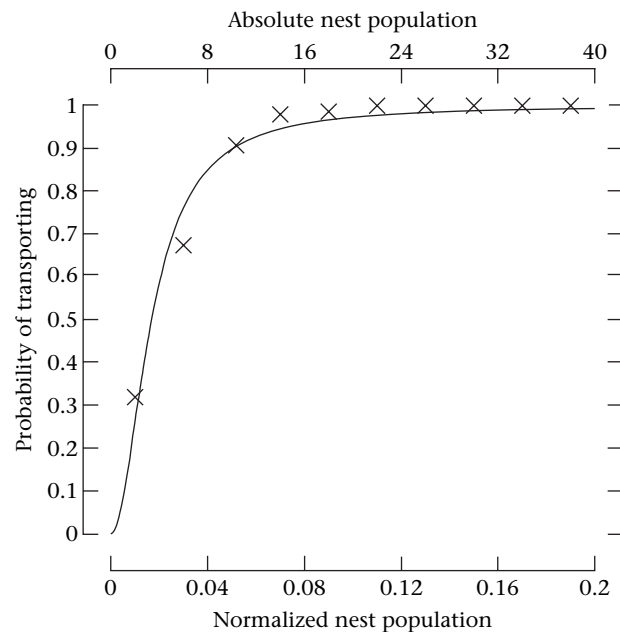


Figure 3. Probability of a recruiter performing a transport rather than a tandem run, as a function of the number of workers at the new site on her immediately previous visit there. Worker numbers are normalized by dividing by total colony population. The upper X axis shows corresponding absolute populations for a colony of average size (200). Crosses show the proportion of transports within equal-sized bins of observed recruitments. The line estimates QuorumMet as a Hill function fitted to these data.

rather than perform another transport. After the first transport in a series, the number of successive transports until the next search can be assumed to follow a geometric distribution with mean μ . The probability of stopping to search after each transport is thus $1/(\mu + 1)$.

TransInNestTime: mean duration of the brief stays inside the new nest between recruitment journeys, during a series of transports.

Reverse: probability that a transport is accompanied by a reverse tandem run, calculated by dividing the number of transport trips that included a reverse tandem by the total number of transport trips.

LostTrans: probability that a reverse tandem follower already committed to the new nest performs a transport if she loses contact with her leader. The estimate was based only on the emigrations by colony 6, in which both old and new nests were videotaped, so that the fate of each follower could be observed.

Model Implementation and Simulation

Based on the flowchart in Fig. 1, an unambiguous description of the model was written in WSCCS, a process algebra for describing systems of interacting agents (Milner 1989; Tofts 1991, 1994; Sumpter et al. 2001). This description (available as electronic Supplementary Material, see below) was then encoded in Objective C to allow computer simulation of both the 12 single-nest and the six two-nest emigrations. The result was a discrete-time agent-based simulation of the flowchart. At each time step, representing 0.1 min of real time, each agent decides its next action. Rate probabilities, such as Accept_i and $\text{Find}_{i,j}$, determine the probability that an agent changes state and yield exponentially distributed persistence times in a given state. Some activities follow other distributions. For example, the durations of individual recruitment trips were sampled from a normal distribution with mean and standard deviation determined by $\text{RecTime}_{\text{Type}}$. Decision probabilities, such as QuorumMet , determine the likelihood that an agent takes a particular branch at a decision point.

In order to compare simulation and data on a colony-by-colony basis, 500 simulation replicates were run for each experimental emigration. Because of the potential importance of colony size to emigration behaviour, each simulation took values of TotalPop and ActiveWorkers from the specific colony to which it was compared (Tables 2, 3). All other parameters took the pooled values in Table 1. The performance of each single-nest simulation was quantified by measuring the time between specific emigration milestones, and by calculating statistics on the distribution of activities among ants. For the two-nest emigrations, the performance statistic was the degree to which the colony split between the two new sites. The distribution of each statistic was constructed from the 500 replicates and compared to the corresponding value measured in the experimental emigrations. The probability P that the observed value follows the same distribution as the simulations was calculated as the proportion of simulations departing as far or further from their mean

than did the experimental value. For example, if a real emigration took 150 min to complete, and 50 of the 500 simulated emigrations took less than or equal to 150 min, then P is 50/500, or 0.1. This yields a two-tailed statistical test, with P less than 0.025 indicating a significant difference between experiment and simulation.

RESULTS

Single-nest Emigrations

Visual inspection of behavioural sequences from real and simulated emigrations suggested similarities in overall pattern (Fig. 4). Once the initial discoveries of the new nest were made, ants led tandem runs from the old nest to the new. Tandems were variable in number, and occasionally completely absent. They eventually gave way to transports, and some of the carried ants themselves went on to transport. From this point, some transporters also led reverse tandem runs from the new nest to the old. Emigrations finished abruptly when the old nest was empty.

The times between four distinct milestones in the real emigrations were mostly within confidence intervals predicted by the model, with two important exceptions (Table 4). First, eight of the 12 real emigrations proceeded significantly faster than predicted by the model, once transport had begun. Second, colony 2, the largest of the six (Table 2), began to transport significantly later than predicted. A colony-by-colony calculation of parameter values showed that colony 2 differed from the others in the lower rate at which its assessors began to recruit to the new nest ($\text{Accept}_{\text{Thin}} = 0.016/\text{min}$; $\text{Accept}_{\text{Thick}} = 0.037/\text{min}$). In simulated emigrations using these values, colony 2 began to transport appreciably later, but still significantly earlier than did the real colony. The remaining difference appeared to lie in the longer time taken by colony 2's explorers to find the new nest (153 ± 79 min, compared to 87 ± 60 for all colonies combined). This slower discovery time could be due either to lower rates of leaving the old nest to search ($\text{Search}_{\text{Explore}}$), or to lower rates of discovery by searchers ($\text{Find}_{0,n}$). The data cannot distinguish these possibilities, because observations necessary to estimate these parameters were made only for colony 6.

Distributions of behaviour across individual ants were generally consistent between model and data. These include the numbers of recruitment acts per ant (Fig. 5a), the numbers of ants performing each recruitment type (Fig. 5b), and the numbers of ants arriving at the new site by different routes (Fig. 6). Both the mean and variation of these measures were well predicted. The only notable difference was the excess of simulated ants leading reverse tandem runs. This discrepancy reflected variation, not incorporated into the model, among real ants in their probability of leading a reverse run. The number of runs per ant departed significantly from the Poisson distribution expected if all ants have the same probability of leading a run on each transport journey ($\chi^2_5 = 47.6$, $P < 0.001$). An excess of ants led no reverse

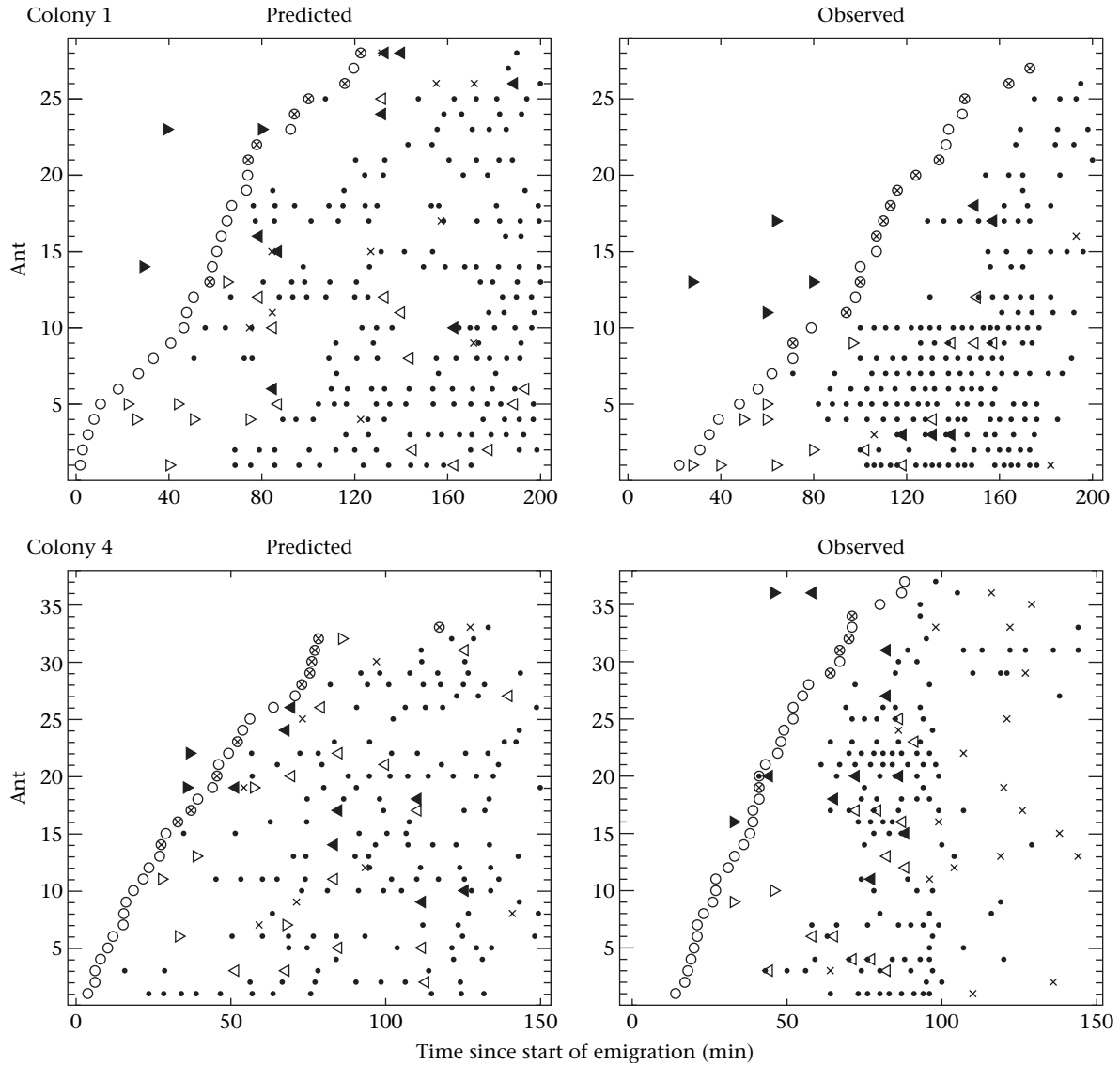


Figure 4. Behavioural sequences of active ants, predicted by the model and observed in single-nest emigrations by colonies 1 and 4. Within each panel, each row shows the acts of a single ant. ○: initial entry into the new nest; ▽: leading a tandem run towards the new nest; ▾: following a tandem run towards the new nest; △: leading a reverse tandem run; ▲: following a reverse tandem run; ●: transporting a nestmate or brood item to the new site; X: being transported into the new site.

tandems, indicating that some ants were more likely than others to lead.

Both simulated and observed emigrations showed considerable interindividual and intercolonial variation. This was seen in the durations of the major stages of emigration (Table 4), as well as the numbers of ants participating in each recruitment type. For example, the numbers of tandem runs varied between 0 and 14 (4.6 ± 5.1) in the 12 real emigrations, and between 0 and 20 (3.2 ± 2.8) in the 6000 simulations.

Two-nest Emigrations

Of the six colonies tested, five moved largely or entirely into the dark nest, as predicted by the model (Table 5). The sixth (A17) moved almost entirely into the light nest, and

remained there for one full day, after which no further observations were made. Four of the five colonies choosing the dark nest experienced some transport to the light nest as well (1 to 39% of brood items). With the exception of colony A4, however, the degree of this splitting was consistent with that predicted by the model (Table 5).

DISCUSSION

Accuracy of the Model

This model tested the hypothesis that colony-level emigration behaviour emerges from interactions among identical individuals following known behavioural rules. In support of this hypothesis, the time course of simulated

Table 4. Durations of intervals between four emigration milestones, as predicted by the model and observed in the single-nest emigrations (boldface)

Colony	First discovery until first tandem run	First discovery until first transport	First transport until 10% transporting	10% transporting until old nest empty
Thin nest				
1	32 41 <i>P</i> =0.25	35 48 <i>P</i> =0.21	31 41 <i>P</i> =0.23	155 149 <i>P</i> =0.40
2	29 28 <i>P</i> =0.53	33 143 <i>P</i> =0.00*	41 36 <i>P</i> =0.38	157 132 <i>P</i> =0.01*
3	35 72 <i>P</i> =0.08	32 51 <i>P</i> =0.10	26 34 <i>P</i> =0.25	131 84 <i>P</i> =0.00*
4	34 No TRs <i>P</i> =0.25	28 19 <i>P</i> =0.26	27 22 <i>P</i> =0.37	109 60 <i>P</i> =0.00*
5	39 41 <i>P</i> =0.47	30 44 <i>P</i> =0.17	13 16 <i>P</i> =0.35	73 37 <i>P</i> =0.00*
6	31 17 <i>P</i> =0.28	30 17 <i>P</i> =0.16	29 33 <i>P</i> =0.35	140 96 <i>P</i> =0.00*
Thick nest				
1	27 7 <i>P</i> =0.06	33 52 <i>P</i> =0.11	28 18 <i>P</i> =0.23	139 157 <i>P</i> =0.06
2	22 31 <i>P</i> =0.18	27 104 <i>P</i> =0.00*	37 43 <i>P</i> =0.28	128 159 <i>P</i> =0.0*
3	28 No TRs <i>P</i> =0.07	27 34 <i>P</i> =0.28	25 33 <i>P</i> =0.21	113 88 <i>P</i> =0.00*
4	30 17 <i>P</i> =0.25	24 25 <i>P</i> =0.42	27 22 <i>P</i> =0.34	91 64 <i>P</i> =0.00*
5	39 No TRs <i>P</i> =0.71	32 25 <i>P</i> =0.39	3 13 <i>P</i> =0.11	81 49 <i>P</i> =0.04
6	25 16 <i>P</i> =0.31	28 49 <i>P</i> =0.05	28 16 <i>P</i> =0.15	118 69 <i>P</i> =0.00*

Predicted values give the mean interval duration, in minutes, of 500 simulations. **P* < 0.05. Tests are two-sided, except for the first milestone in emigrations lacking any tandem runs (No TRs). Those tests are one-sided, with *P* calculated as the proportion of simulations in which no tandem run was observed.

single-nest emigrations generally conformed to experimental data, with the notable exceptions of the rate at which colony 2 initiated recruitment and the rate at which most colonies completed the transport phase. The model also successfully predicted the distribution of behaviour across individual ants in the single-nest emigrations, except that it overestimated the number of reverse tandem leaders. These moderately good matches may seem unsurprising given that these data were also

used to parameterize the model. It does not necessarily follow, however, that the resulting simulations should resemble the observed emigrations. Parameter values were derived from measurements of individual behaviour, such as rates of recruitment initiation and responses to nest population, rather than colony properties, such as emigration duration and the distribution of recruitment activity across ants. That the simulations were nevertheless able to reproduce these global properties, as well as generating believable sequences of individual behaviour, counts as good evidence that the model has captured the fundamental components of the colony's collective behaviour.

A more stringent test of the model's adequacy was made by comparison to the two-nest emigrations, which were not used for parameter estimation. This comparison focused on the degree to which the colony split between two alternative sites. The model predicted that roughly 10% of each colony should typically be carried to the worse nest by the time the old nest is completely empty. The match between predictions and experiments was more equivocal than for the single-nest data. Although experiments confirmed the high prevalence of splitting, its magnitude was less well predicted, with four colonies splitting as expected, a fifth nearly so, and one colony moving almost entirely into the worse nest.

Individual and Colony Variation

All individuals in this model behaved according to identical parameter values derived from data pooled across many workers and colonies. Real ants, of course, are highly variable, which may in turn cause significant variation in colony properties. An interesting possibility, however, is that some variation observed at the colony level does not reflect individual differences, but instead emerges from interactions among identical ants. Our simulations support this idea, because they preserve much of the variation seen among real colonies, despite using identical parameter values for all ants. For example, both model and data showed a significantly skewed division of labour (Fig. 5a), with a few ants disproportionately active in recruitment. Likewise, both real and simulated emigrations showed large variation in the amount of tandem running and the times at which various stages of the emigration began.

On the other hand, the lack of explicit individual variation in parameter values may account for the model's failure to predict some differences among colonies. In particular, if workers behave differently according to the size of their colony, then our parameter estimates may not adequately describe the behaviour of ants in colonies of all sizes. The colonies used to estimate parameters varied from 38 to 158 workers, and those used in the splitting experiments from 98 to 174 workers. Colony 2, the largest of the former group, started transport significantly later than predicted. Colonies A4 and A17, the largest of the latter group, were the only ones departing significantly from the predicted degree of splitting. Indeed, the performance of A4 and A17 clearly goes against the model's

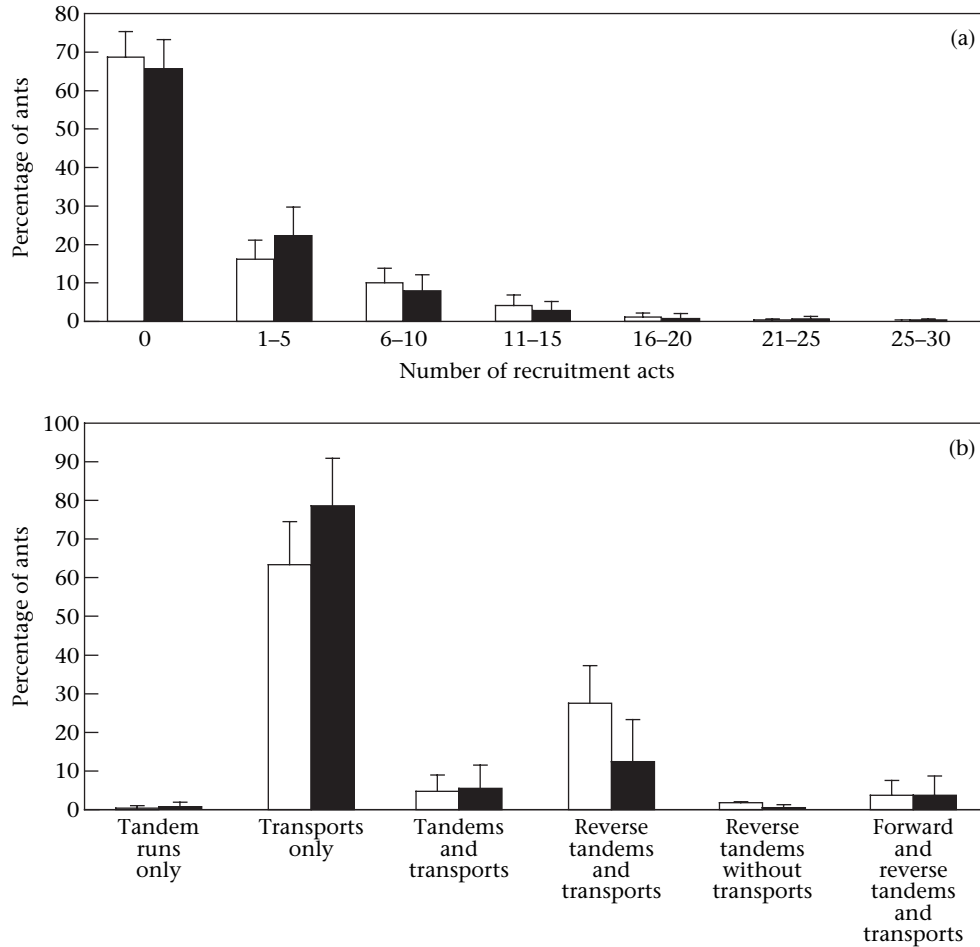


Figure 5. Distribution of recruitment behaviour across ants in single-nest emigrations, for simulations (□) and observations (■). (a) Number of recruitment acts by each ant. (b) Type of recruitment act performed by each ant. Error bars show standard deviations.

prediction that larger colonies should end up with slightly higher proportions in the better nest than smaller colonies. The behaviour of colony 2 arose in part because its workers initiated recruitment much more slowly than did those of other colonies. This reluctance to recruit suggests that workers judged the nest to be of low quality, perhaps because they found it too small to house them adequately. Also implicated are lower rates of search initiation at the old nest, or lower rates of discovery by searchers, based on the unusually long time taken by active ants to find the new nest. Similar factors do not seem likely to explain the discrepancies seen in the splitting experiments. If anything, lower search and acceptance rates are expected to reduce splitting (D. J. T. Sumpter & S. C. Pratt, unpublished data). Further experiments with more observations over a broad range of populations will be required to explicitly test how colony size may affect splitting among sites.

Besides colony size, other sources of interindividual variation may be at work. The quicker-than-predicted finish of most observed emigrations could reflect variation in recruitment speed. Ants with a high tempo of recruitment would contribute disproportionately to the final stage of transportation. Likewise, differences in the

experience of individual ants could explain the lower-than-predicted number of reverse tandem run leaders. Although the function of reverse tandem runs remains unknown, a plausible role is to allow ants with a good knowledge of the route between old and new nests to inform nestmates following worse routes. If so, leadership of reverse runs may be concentrated in a subset of better-informed navigators.

Applications of the Model

Given a model that reasonably depicts reality, its future value will come from performing 'what if?' simulations that test the effect of alternative parameter values and decision rules on colonial decision making. Even in developing the model, this approach helped us to identify the importance of particular behavioural rules. For example, achieving a good qualitative fit to the data required both the graded commitment strategy of active ants and the ability of individuals to compare two sites and choose the better one. These tests partly justify the numerous behavioural states and complex transition patterns in Fig. 1, but they cannot rigorously prove the necessity of

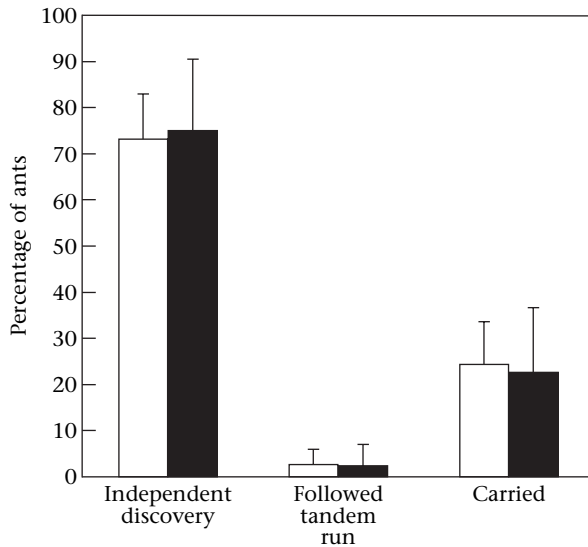


Figure 6. Distribution of the routes by which ants found the new nest in single-nest emigrations, for simulations (□) and observations (■). Error bars show standard deviations.

the behavioural algorithm. At this point we can only say that statistical comparison of simulations and experiments does not reject the hypothesis that the model is a sufficient explanation of the data. Future work will concentrate on using the model to make testable predictions about how emigrating colonies respond to different sets of options and different conditions at the old nest.

A surprising model prediction, which we were able to test and confirm experimentally here, was the high prevalence of splitting between sites. One might expect the colony's decision-making algorithm to avoid splitting, because of the cost of secondary emigrations needed to restore colony unity as well as the danger of permanent separation. If, however, this cost is balanced by more rapid escape from dangerous exposure at the old nest, then the optimal strategy may involve some splitting. Indeed, recent work suggests that the degree of splitting may be a flexible feature of the colony's decision making, with individual workers modulating their behaviour to trade off speed and accuracy of decision making (Franks et al. 2003a). In particular, ants may switch to transport at a lower quorum size (i.e. smaller QuorumMet) when conditions at the old nest are especially bad, an adjustment

Table 5. Predicted and observed percentages of brood items located in the superior (dark) nest once the old nest was emptied, for the two-nest emigrations ($\bar{X} \pm SD$)

Colony	% Predicted	% Observed	P
A4	96 ± 5	61	0.00*
A6	95 ± 6	80	0.04
A8	95 ± 7	99	0.34
A14	96 ± 5	98	0.57
A16	93 ± 8	100	0.09
A17	96 ± 5	2	0.00*

* $P < 0.05$.

that could allow them to evacuate the old nest more quickly, but at the cost of a less accurate choice.

Model Complexity

The model presented here contains many parameters and behavioural states. Had we estimated parameter values by seeking the best match between predicted and observed colony-level properties, then we would have run the risk of overfitting the model. We avoided this problem by instead estimating parameters independently of the statistical measures used to test the model. As a result, adding parameters does not increase the likelihood of falsely accepting a match between predictions and observations, and thus wrongly concluding that the model adequately captures the ants' behaviour. In fact, the opposite was true, because each additional parameter increased the constraints on the model's colony-level behaviour. Thus, as we gather more information about the system, the likelihood of falsely accepting a match decreases.

On the other hand, it should not be assumed that all parameters contribute equally to colony-level performance. Some may prove to be relatively unimportant details. Our goal, however, was not a simple phenomenological model capturing one or two properties of nest choice (as in Pratt et al. 2002). Instead we aimed to capture the whole of our current understanding of the system in a model that was fully consistent with the data. In this we have followed a tradition well developed in the modelling of biochemical (Barkai & Leibler 1997), gene regulatory (von Dassow et al. 2000) and other complex networks (Kitano 2002). By identifying all known communication pathways among individuals, this approach allows for meaningful analysis of how each pathway contributes to overall system function (Fewell 2003). Ultimately, the exact role of different parameters can be tested through a robustness analysis, whereby we systematically change model parameters and monitor the effect on colony behaviour. By doing this work in tandem with experimental studies, the model can be revised and in turn inspire still more experiments. Social insects are an ideal system for this approach to complex networks, because they are open to in situ observation and manipulation of individually marked network components.

Individual- versus Colony-level Complexity

Temnothorax show a high degree of individual sophistication in their ability to assess candidate nests and accordingly regulate their recruitment behaviour (Mallon & Franks 2000; Mallon et al. 2001; Mugford et al. 2001; Pratt & Pierce 2001; Pratt et al. 2002; Franks et al. 2003b). These complicated behavioural rules are in stark contrast to the 'simple rules of thumb' often proposed to explain aggregation of insect groups (Deneubourg et al. 2002; Jeanson et al. 2004) and collective decision making by insect societies (Detrain & Deneubourg 2002). The philosophy of much of this work holds that simple individual rules can generate complex group patterns (Detrain et al. 1999; Camazine et al. 2001; Sumpter & Pratt 2003). The

contrast with our model partly reflects a tendency of many studies of self-organization to underestimate the behavioural complexity of individual animals (Seeley 2002). At the same time, it may also point to real differences in the individual complexity required to generate group functions in different contexts. Unlike decisions among food sources, the choice of a nest requires unanimity, if the ants are to avoid colony division (Franks et al. 2002). A simple competition between independent recruitment processes may fail to achieve this result reliably. Furthermore, the small size of *Temnothorax* colonies precludes the strong positive feedback of mass recruitment by pheromone trails central to the cohesive migration of large colony species such as army ants (Topoff 1984; Beekman et al. 2001).

Debate about whether behavioural complexity lies within the cognitive abilities of individual insects or arises from repeated nonlinear interactions between them should not obscure the importance of establishing the precise behavioural mechanisms by which insect societies function. In this paper we have shown how sufficient individual-level data makes possible the determination of an algorithmic form for the behaviour of emigrating ants. Similar experimental data is also available for honeybee house-hunting (Camazine et al. 1999; Seeley & Buhman 1999; Seeley & Buhman 2001; Seeley 2003; Seeley & Visscher 2003, 2004) as well as for certain aspects of the foraging of honeybees (Seeley 1995) and several ant species (Detrain & Deneubourg 1997; Maillieux et al. 2000, 2003). By organizing this information in algorithmic models, which can then be validated against further experimental data, we can systematically compare the algorithms used by different insect societies to solve a variety of problems. Such a comparison ultimately can reveal not only how social insects solve difficult general problems (Bonabeau et al. 1999), but also how evolution has shaped appropriate solutions to the specific challenges encountered by different societies.

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Supplementary Information

Supplementary information associated with this article can be found, in the online version, at [doi:10.1016/j.anbehav.2005.01.022](https://doi.org/10.1016/j.anbehav.2005.01.022)

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