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Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*

Abstract Social insect colonies possess remarkable abilities to select the best among several courses of action. In populous societies with highly efficient recruitment behaviour, decision-making is distributed across many individuals, each acting on limited local information with appropriate decision rules. To investigate the degree to which small societies with less efficient recruitment can also employ distributed decision-making, we studied nest site selection in *Leptothorax albipennis*. Colonies were found to make sophisticated choices, taking into account not only the intrinsic qualities of each site, but also its value relative to the available options. In choices between two sites, individual ants were able to visit both sites, compare them and choose the better one. However, most ants encountered only one site in the course of an emigration. These poorly informed ants also contributed to the colony's decision, because their probability of initiating recruitment to a site depended on its quality. This led to shorter latencies between discovery and recruitment to a superior site, and so created greater amplification via positive feedback of the population at the better site. In short, these small colonies make use of a distributed mechanism of information processing, but also take advantage of direct decision-making by well-informed individuals. The latter feature may in part stem from the limitations of their social structure, but may also reflect the stringent demand for unanimous decisions by house-hunting colonies of any size.

Keywords Communication · Decentralised control · Social insects · Ants · Decision-making

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Introduction

Social insects have special importance for the study of decision-making, because they make choices not only as individuals, but also collectively. A foraging honey-bee decides whether and how much to exploit a given flower patch on the basis of patch quality and information about colony and environmental conditions (Schmid-Hempel et al. 1985; Eckert et al. 1994). At the same time, her colony as a whole decides how to apportion workers among the many patches its foragers have found (Seeley 1995). The collective decision is not a mere summation of choices made by individual insects; the colony can discriminate between two food sources of different quality, even when no single forager has sampled more than one (Seeley et al. 1991). Rather, a global decision emerges from the interactions of many workers, each possessed of limited local information, and acting on it with appropriate decision rules.

Most research on collective decision-making has focused on populous societies with efficient recruitment tools, such as the waggle dance of the honey-bee and the trail pheromones of many ants (Beckers et al. 1990; Seeley 1995; Bonabeau et al. 1997). Large colony size and effective recruitment are important components in the mechanisms of collective action described to date. Recruitment generates positive feedback that can amplify small differences among colony options (Beckers et al. 1990). Population size matters because workers rely on rates of interaction with nestmates for indirect cues about colony and environmental state (Seeley 1992; Pacala et al. 1996; Gordon and Mehdiabadi 1999; Jeanne 1999). Large population size buffers a colony against stochastic effects on interaction rates that can degrade the quality of information available to each insect.

Decision-making by smaller and less integrated insect societies has attracted much less attention. Many ant colonies, including members of the genus *Leptothorax*, number only a few hundred workers. These ants typically recruit via tandem running or social carrying, which can summon only one nestmate at a time (Beckers et al.

1989; Möglich 1978). Can these simpler societies accomplish the same collective behaviours as more complex colonies? If so, what are the underlying mechanisms? Small colonies may instead place a greater cognitive burden on individual workers. However, the actual balance between individual and collective action, and the ways in which these interact, remain open questions. Small colonies offer practical advantages for analysing social organisation, because all the workers can be individually marked, and the behaviour of any given worker described in detail. This approach has successfully been applied to many aspects of social behaviour in *Leptothorax* (Franks and Sendova-Franks 1992; Sendova-Franks and Franks 1993, 1999; Franks and Deneubourg 1997).

In this paper, we analyse the behavioural mechanisms of nest site selection in *Leptothorax albipennis*. These ants typically form colonies of fewer than 300 workers and do not produce pheromonal recruitment trails. They nest in preformed rock crevices, and must frequently emigrate when their old nest deteriorates or its capacities are outstripped by colony growth (Partridge et al. 1997). In the laboratory, when emigrating colonies are given a choice between nest sites of different area, they reliably reject those below a certain size (Mallon and Franks 2000).

Previous research on *L. albipennis* and other *Leptothorax* species has sketched a basic picture of how colonies organise emigrations (Möglich 1978; Sendova-Franks and Franks 1995). Any given emigration is carried out by a minority of active ants, with most workers remaining entirely passive, neither searching for nor recruiting to new nest sites. When an active ant discovers a potential site, she evaluates it at length, and then begins to lead tandem runs, a recruitment method by which a single ant is led all the way from the old nest site to the new one (Möglich et al. 1974). Some of these recruits also lead tandem runs, and the population at the new site gradually increases. Eventually, the active ants cease leading tandem runs from the old nest and simply carry the remaining ants and brood items, one at a time. During this transport phase, some of the active ants also lead tandem runs from the new nest back to the old.

Here we investigate the kinds of decision-making abilities colonies possess, and the individual behaviours that underlie them. In particular, we ask whether colonies can make context-dependent decisions about nest site quality, actively comparing the available options and choosing the best one. If so, do their abilities follow simply from comparisons made by individual ants, or are more distributed mechanisms at work? Specifically, do ants show quality-dependent recruitment to nest sites in a way that could underlie differential positive feedback to sites of different quality?

Methods

Collection and housing of colonies

Colonies of *L. albipennis* were collected from Portland Bill, England, in July 1998, April 1999 and February 2000. Each colony was housed in a nest made by sandwiching a cardboard perimeter (1.6 mm thick) between two glass microscope slides (50×76 mm). Ants accessed the rectangular nesting cavity (33×25 mm) through a single entrance 2 mm wide, 1.6 mm high and 2 mm long. Each nest was placed in a Petri dish (100×100×17 mm), the walls of which were covered with Fluon to prevent the ants escaping. All colonies had queens, and worker populations ranged from 37 to 158, with a median value of 97.

Identification of mediocre nest design

To study the decision-making ability of a colony we must present it with a non-trivial choice. That is, we would learn little if, presented with two alternatives, the ants do not recognise one as a prospective nest. Thus we began by identifying a mediocre nest site design; i.e. an acceptable design that colonies nonetheless reject if offered a better option.

We designed candidate mediocre sites by manipulating the cavity floor area, the cavity height and the entrance size of artificial sites. Earlier work had already shown that ants prefer a floor of 912 mm² to one of half that area (Mallon and Franks 2000). We hypothesised that ants would prefer the spaciousness of a broad and thick cavity, and the improved defensibility of a small entrance. Thus we chose as a superior nest site one with a floor area of 825 mm² (25×33 mm), a cavity height of 1.6 mm and an entrance 2 mm wide. We then created two alternatives which departed increasingly from the superior design: (1) a site with the floor area and entrance size of the superior site, but with a thickness of only 0.8 mm, and (2) a site with a thickness of only 0.8 mm, as well as a smaller floor area (414 mm², 18 ×23 mm), and a wider entrance (23 mm).

A colony in its original nest was placed against the centre of one wall of a large square Petri dish (220×220×17 mm). Two new nest sites of different design were placed in opposite corners of the dish, equidistant from the old nest (10 cm from entrance to entrance). The combinations were (1) alternative 1 versus alternative 2 or (2) alternative 1 versus the superior nest. We initiated an emigration by removing the roof of the old nest. After 2 days, we noted which new site the colony had occupied. A colony was deemed to have chosen a site if it contained all the ants bar a few foragers. Each comparison was repeated with 14 colonies. Half were presented with one left-right ordering of the alternative nest sites, and half with the other, to control for any directional biases. A binomial test determined whether colonies chose one design over the other significantly more often than expected in the absence of a preference.

Videorecording of emigrations

We performed two experiments in which we videotaped emigrations by colonies of individually marked ants, so that we could describe in detail the behaviour of each active ant. In the first experiment, designed to determine whether individual ants visit multiple sites and compare them during an emigration, three colonies were induced to choose between a mediocre and a superior site. In the second experiment, designed to determine whether the speed or intensity of recruitment varies according to the quality of a nest site, six colonies were induced to emigrate twice: once to a mediocre and once to a superior site.

In each colony, every ant was marked with four tiny paint marks: one spot each on the head and thorax and two on the gaster (Sendova-Franks and Franks 1993). Emigrations were carried out in a large Plexiglas arena (75×43×7 cm) carpeted with paper. For emigrations in which two new sites were offered, the original nest was placed against the centre of one wall of the arena, and the new sites were placed in opposite corners. Each new site was 45 cm from the old nest. For emigrations in which only one new site was offered, the original nest and the new site were placed against opposite walls of the arena, 65 cm apart.

Throughout the emigration, a digital video camera (Panasonic NV-DS1 or JVC GRDV3ek) was trained on the interior of each new site. From the resulting videotapes, we transcribed for each

ant all of her entries, exits and carrying behaviours. The video-tapes did not capture every tandem run, since these often broke up or changed followers in the arena, beyond the camera's view. Hence, observers watched the arena and the old nest throughout the emigration, recording on the audio channel of the videotape both the timing and participants of each tandem run.

Results

Identification of mediocre nest design

In the first choice experiment, 11 colonies out of 14 chose alternative 1 over alternative 2 (Binomial test: $P<0.05$, $n=14$). In the second experiment, 14 out of 14 colonies chose the superior site over alternative 1 (Binomial test: $P<0.0001$, n=14). Thus alternative 1 – a thin cavity of large area with a small entrance – fulfills the requirements of a mediocre site.

Dynamics of nest site choice

When colonies were offered a choice between a superior and a mediocre site, the population increased dramatically only at the superior site, to which the bulk of the ants were moved within 2–5 h (Fig. 1). Detailed plots of each active ant's behaviour throughout the emigration (Fig. 2) show that both kinds of site were visited by several ants in the course of each emigration, but only 13 ants recruited to the mediocre sites versus 116 to the superior ones. Colony 1 showed the strongest recruitment to the mediocre site, to which it transported 16 adults and 13 brood items. These were subsequently retrieved by active ants from the superior site, once the old nest had been completely emptied (for example, ants 1, 14, 19 and 27).

Comparison of nest sites by individual ants

One way that the colony could compare two nest sites is for each active ant to visit both and choose the better one. That is, the process might not be a collective decision at all, but rather an individual decision iterated over many ants.

In three choices between a superior and a mediocre site, a total of 66 active ants visited both sites, and thus had an opportunity to compare them. Of these ants, 38 were exposed to both sites, either by walking (30) or being carried into them (8), before beginning to recruit to either of them. If these ants compare sites directly, we would expect them to confine their subsequent recruitment to the better site. Indeed, 35 of the 38 initiated recruitment only to the superior site (for example, ants 3, 6 and 18 in colony 1; ants 2, 12 and 13 in colony 2; and ants 2, 4 and 7 in colony 3; Fig. 2) The remaining 3 led a few tandem runs to the mediocre site before switching their recruitment to the superior site (ants 7, 22 and 27 in colony 3).

Ten ants began recruiting to the better site and then found the mediocre one (for example, ant 28 in colony 3; Fig. 2). All ten continued to recruit only to the superior
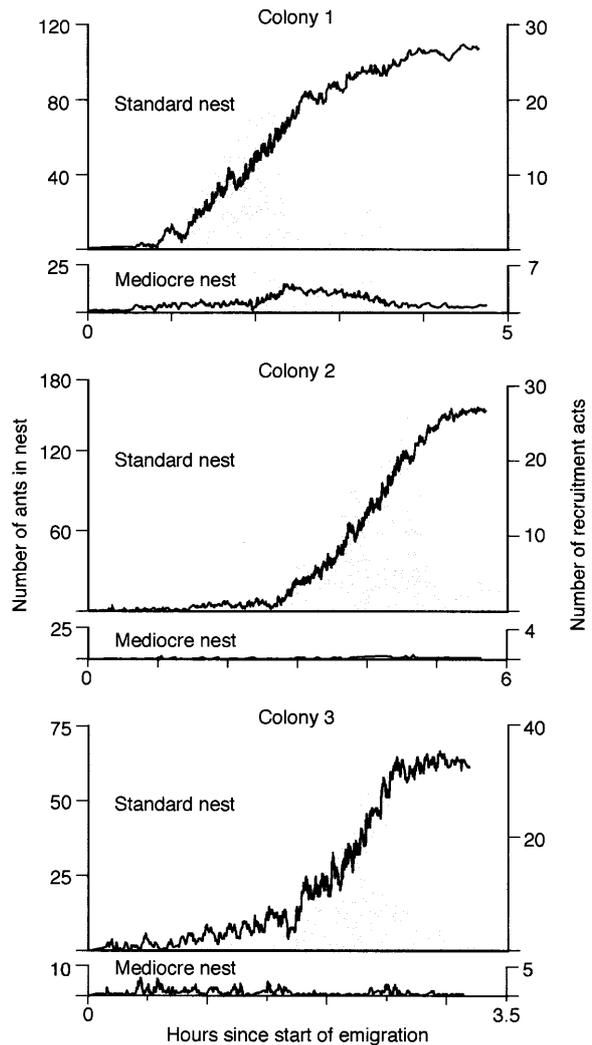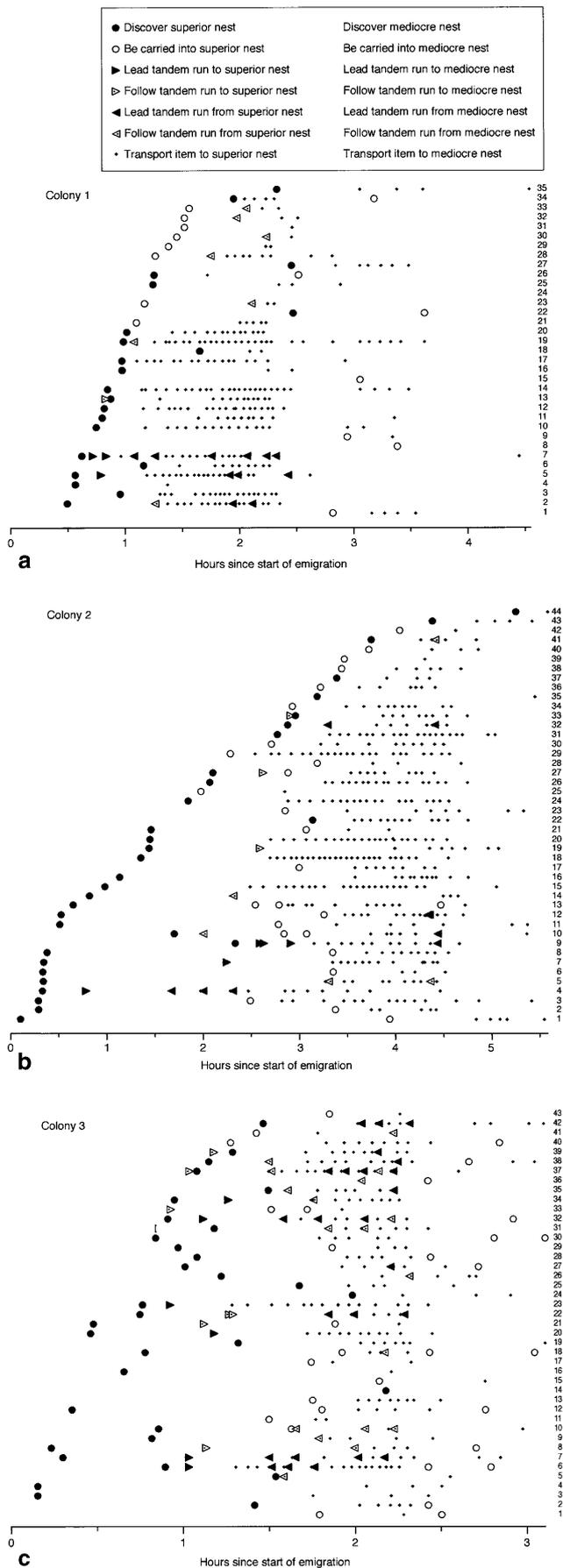

Fig. 1 Recruitment and population dynamics for colonies choosing between a superior and a mediocre site. For each site, *grey bars* show the number of recruitment acts (tandem runs and transports) per 5-minute period. *Black lines* show the worker population

site. In contrast, four out of the five ants that began recruiting to the mediocre site, and then found the superior one, switched their allegiance (for example, ant 27 in colony 1; Fig. 2). This shows a significant difference between the propensity to switch in these two situations (Fisher's exact test: $P<0.01$).

The opportunity for individual comparisons varied considerably across colonies. In colony 3, 86% of eventual recruiters visited both sites at some point during the emigration ($n=43$), but in colony 2, only 32% did so ($n=44$). In colony 1, the value was 46% ($n=35$). Thus, two colonies were able to choose the better site, even at moderate levels of individual comparison.

Influence of nest site quality on recruitment behaviour

Ants that visit only one site may nonetheless contribute to the colony's decision, if their response to a site

● Discover superior nest · Discover mediocre nest
○ Be carried into superior nest · Be carried into mediocre nest
▶ Lead tandem run to superior nest · Lead tandem run to mediocre nest
▷ Follow tandem run to superior nest · Follow tandem run to mediocre nest
◀ Lead tandem run from superior nest · Lead tandem run from mediocre nest
◁ Follow tandem run from superior nest · Follow tandem run from mediocre nest
· Transport item to superior nest · Transport item to mediocre nest

Colony 1

a Hours since start of emigration

Colony 2

b Hours since start of emigration

Colony 3

c Hours since start of emigration

depends on its quality. For example, a better site might induce faster or more intense recruitment, and thus experience more rapid population growth, than a poorer site.

To discover whether such changes exist, we induced each colony to emigrate twice, once to a mediocre and once to a good site. Comparison of population growth in each pair suggested more rapid growth at the better site (Fig. 3). From the videotapes of the second set of video-taped emigrations (one nest site offered), we examined four aspects of ant behaviour that might contribute to the effectiveness of recruitment. The number of recruiters was simply calculated as the total of all ants that led tandem runs or transported any nestmates or brood during the emigration. Both transport and tandem runs were included in recruitment, because these are the means by which passive colony members and active ants, respectively, are brought to the new nest site. Although the number of recruiters varied across colonies, ranging from 26 to 48% of colony population, it showed no dependence on site quality (Wilcoxon signed-ranks test: $T=-0.135$, $n=6$, $P=0.892$). The recruitment effort was defined as the number of tandem runs and transports by each recruiter. The recruitment rate was estimated by measuring each interval from the beginning of one recruitment act to the beginning of the same ant's next recruitment act. For each ant, the median of all such intervals was calculated, and its reciprocal taken as the recruitment rate. Neither effort nor rate differed between emigrations to mediocre and superior sites (Tables 1, 2).

Finally, we measured recruitment latency, the time between each ant's first entry into a site and her first recruitment to it. Using these data, we calculated survivorship curves depicting the rate of decrease in the population of active ants assessing a site, as each ant began to recruit (Fig. 4). This method of analysis allowed us to take into account active ants that entered the new site, but had not yet begun to recruit at the end of the emigration. Survivorship curves were fitted via the Kaplan-Meier method (Lee 1980), and ants were excluded from the analysis if both of the following conditions were met: (1) they had been carried into the new nest site by another ant, rather than walking on their own power, (2) they had never themselves recruited a nestmate, transported a brood item or followed a tandem run.

Three of the six colonies had significantly steeper survivorship curves for better nest sites than for mediocre ones, by a generalised logrank test (Lee 1980) (Fig. 4). Two other colonies showed a non-significant trend in the same direction. A steeper slope indicates a higher probability that an ant will begin recruiting at any given time. For each colony, we can estimate this probability as the inverse of the mean recruitment latency. This gives

Fig. 2 Detailed behaviour of recruiters during the same choice tests shown in Fig. 1. Each *line* represents a single ant, identified by a number at the *right*. *Symbols* show the start time of each act. Behaviours associated with the superior and mediocre nest site are indicated by *black* and *grey* symbols, respectively

Fig. 3 Population growth at the new nest site during emigrations in which only one new site was available. Each colony emigrated twice, once to a superior site (*black lines*) and once to a mediocre site (*grey lines*)
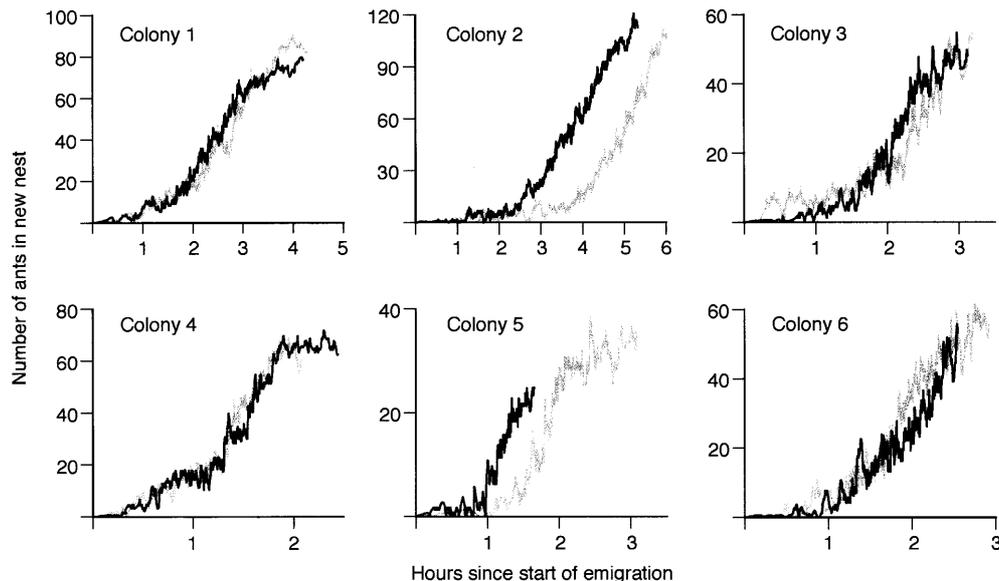

Fig. 4 The number of ants not yet recruiting as a function of time since each ant first entered the nest site, for the emigrations shown in Fig. 3. Emigrations to superior and mediocre sites are shown by *solid* and *dashed lines*, respectively. The latency between entry and recruitment (mean±SD), and the number of ants analysed, are shown next to the corresponding survivorship curve. For each emigration, the χ^2-value and corresponding *P*-value show the result of a generalised logrank test comparing latencies for the mediocre and the superior site
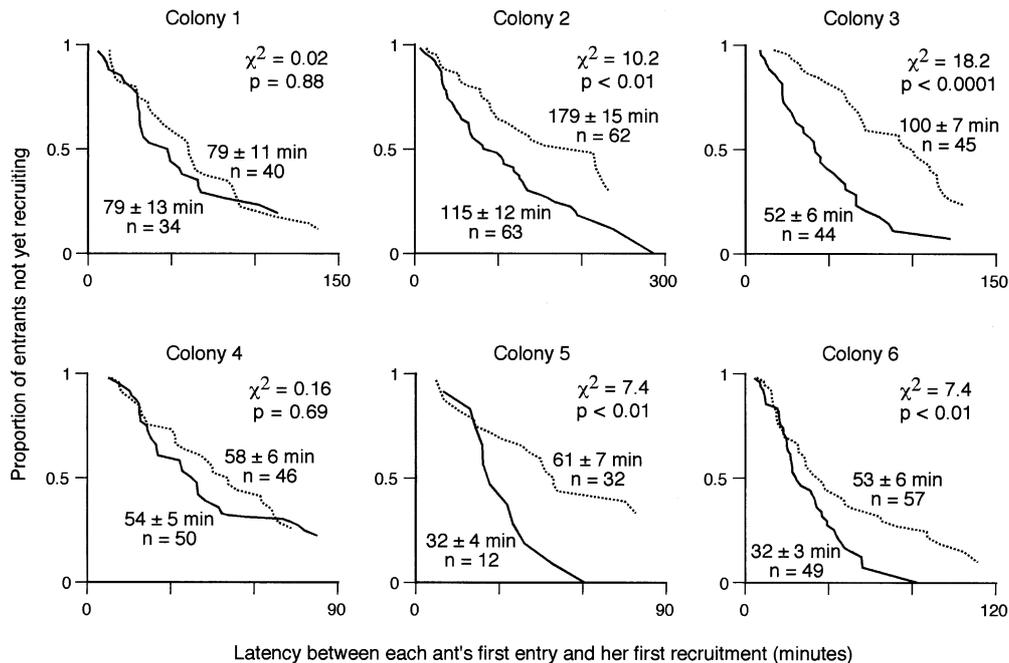

Table 1 The median number of recruitment acts by individual ants during emigrations to superior (*S*) and mediocre (*M*) nest sites, compared by a Mann-Whitney *U*-test

Colony	Superior	Mediocre	n (S, M)	U	P
1	6	4.5	27, 36	873.5	0.9005
2	4	7	51, 33	2013	0.1584
3	3	4	37, 32	1,176.5	0.1556
4	3	5	35, 29	1,007.5	0.3844
5	3	2	11, 20	186.0	0.6855
6	5	5	45, 45	2,070.0	0.8591

Table 2 The median intervals between recruitment acts for individual ants during emigrations to superior and mediocre nest sites, compared by Friedman's ANOVA (*S*), with 1 *df*. No results are shown for colony 5, because it contained no ants involved in emigrations to both the mediocre and the superior site

Colony	Median (min)		S	n	P
	Superior	Mediocre			
1	7.0	9.3	4	16	0.046
2	9.9	8.7	3.77	13	0.052
3	7.8	7.7	0.08	13	0.782
4	6.2	6.5	0.69	13	0.405
6	8.0	8.6	1.92	13	0.166

values from 0.87×10^{-2} to 3.2×10^{-2} min^{-1} for superior sites and 0.54×10^{-2} to 2.2×10^{-2} min^{-1} for mediocre sites. These probabilities differ significantly between site types (Wilcoxon signed ranks, $P<0.05$), with a mean ratio of superior site probability to mediocre site probability of 1.4 ± 0.3 (mean$\pm$SD). These results suggest that an ant arriving at a superior site begins recruitment sooner, on average, than an ant arriving at a mediocre site.

Discussion

When offered a choice between two nest sites of different quality, colonies of the ant *L. albipennis* reliably choose the superior site, despite the apparent limitations imposed by their small colony size and relatively simple recruitment system. This decision emerges in part from direct comparisons made by individual ants that have visited both sites. However, ants that have visited only one site also contribute to the decision, because they take less time to initiate recruitment to a superior than to a mediocre site. This difference is the basis of positive feedback that drives up recruitment more rapidly to better sites than to worse ones. We propose that the colony's decision emerges from a combination of this distributed process, and the ability of some ants to make direct comparisons.

In making their choice, colonies do not merely satisfice, taking the first option that surpasses a threshold quality. Under such a strategy, statistically half of the colonies should have chosen the mediocre site when it was offered with the superior one. Two important conclusions about the colony's decision follow from these results. First, the ants somehow integrate several aspects of nest site design – floor area, cavity height and entrance size – rather than depending on a single key characteristic. Second, they take into account not only intrinsic qualities of each site, but also its value relative to the available options. These abilities are on a par with those achieved by house-hunting honey-bee swarms, with their greater populations and more complex recruitment communication (Seeley 1985; Seeley and Buhrman 2001).

Direct comparisons by individual ants

Can individual ants really compare nest sites and choose the better one? The biased choices made by ants that have visited both sites suggest that they can. However, we must also consider a simpler hypothesis based on the fact that individual recruitment latencies follow an approximately exponential distribution (R^2 ranges from 0.53 to 0.99). For a given site quality, the rate constant of this distribution gives the probability per time step that an ant will start to recruit. This allows us to model the initiation of recruitment as a Poisson process, analogous to radioactive decay. Each process begins as soon as an ant discovers a site, and ends when she begins to recruit to it. If she discovers two nests, then two independent processes run in parallel. The ant eventually chooses the nest corresponding to the process that happens to complete first. Because of its higher rate constant, the better site will be chosen more often, even though the ant treats each site no differently than she would if it were the only one she had found. It does not matter which site the ant discovers first, or how much time separates the two discoveries. The "memoryless" property of the exponential distribution means that the ant's instantaneous probability of recruitment initiation remains unchanged no matter how much time has passed since she first entered the site.

To show that this plausible mechanism is not in fact employed, we calculated the proportion of ants discovering both sites that are expected to recruit to the superior one:

$$P(X_s < X_m) = \frac{\dfrac{1}{\tilde{X}_s}}{\dfrac{1}{\tilde{X}_s} + \dfrac{1}{\tilde{X}_m}}$$

where $\tilde{X}_s$ and $\tilde{X}_m$ are the mean individual recruitment latencies for the superior and mediocre sites. These values were estimated as 51 and 97 min, respectively, from the data for colony 3 (Fig. 4). This provided a conservative test, because colony 3 had the largest observed ratio of mean latencies between site types. Of the 66 ants that visited both sites at some point during an emigration, 30 independently walked into each site before beginning to recruit. Under the "no-comparisons" model, 19.7 of these should have chosen the superior site and 10.3 the mediocre one. These numbers differ significantly from the observed values of 27 and 3 ($\chi^2=7.9$, 1 *df*, $P<0.01$). This shows that ants do indeed actively compare sites and choose the better one.

Collective decision-making

Individual comparison of nest sites does not completely describe the decision-making seen in our experiments. All three colonies chose the better nest, but two were able to do so even though a majority of their recruiters visited only one site. The third case, in which over 80% of the recruiters encountered both sites, may not be the most typical situation in nature. By offering only two alternatives in a small arena, we probably increased the number of independent discoveries of both sites, relative to that expected in a larger and more complex natural environment.

The bulk of poorly informed ants still contribute to the colony's choice, through a distributed process reminiscent of decision-making in large-colony species. A crucial ingredient in these cases is the dependence of recruitment strength on target quality (Detrain et al. 1999). This allows positive feedback to amplify small differences in individual assessment of a target, even in the absence of direct comparison by individuals. For example, *Lasius niger* deposit more pheromone on

recruitment trails to better food sources (Beckers et al. 1993), and honey-bees encode food quality by the strength of their dancing, which feeds forward into the number of bees recruited (Seeley et al. 2000).

In *L. albipennis*, the number of recruiters, the rate at which they work and the amount of work performed by each does not depend on nest site quality. Instead, the results suggest that site quality determines each ant's instantaneous likelihood of initiating recruitment, and thus the average latency until an ant begins to recruit to a site she has found. This difference in latencies could then cause stronger positive feedback on recruitment to better finds. Moreover, by delaying recruitment to worse sites, the ants buy time in which to discover alternatives. At the same time, because recruitment eventually begins even to a poor site, the colony does not remain homeless, if nothing better can be found.

The clear role for individual decision-making in these ants makes an interesting contrast with honey-bees, the only other insect society in which house-hunting has been studied in detail (Lindauer 1961; Camazine et al. 1999; Seeley and Buhrman 1999, 2001). Like the ants, bees rely on a relatively small number of active workers that search for potential sites and then recruit to them, in the bees' case via waggle dances. Unlike the ants, dancers seldom switch their allegiance from one site to another. Instead, the advertisers of rejected sites simply cease to recruit altogether (Camazine et al. 1999; Seeley and Buhrman 1999). A small number of bees do visit more than one site, hence a role for individual comparison cannot yet be ruled out. Nonetheless, experimental evidence suggests that these multiple visits are unnecessary for effective decision-making, at least in the simplified context of a choice between two identical sites (Visscher and Camazine 1999).

There are two reasons why *L. albipennis* colonies may depend more on individual comparisons than do bees. First, distributed information-processing may be less efficient in small societies. Perhaps a large population of relatively ignorant honey-bees can achieve the twin goals of selecting the best site and also avoiding deadlock or colony division. A small colony of *L. albipennis* may need an additional component of direct comparison by well-informed individuals.

Second, the bees, unlike the ants, clearly separate decision-making from emigration. The swarm lifts off only after a consensus has been reached by the dancers, and every bee flies under her own power. In the ants, most colony members are transported passively, and such transports are one of the means by which an active ant casts her vote for a site. If an active ant dropped out of recruitment entirely, as bees do, she might help the colony reach a consensus, but she would also retard the actual emigration. Instead, individual ants make direct comparisons, change allegiance, and thus continue to help move the colony.

The overlap between decision-making and moving means that ants sometimes transport colony members to more than one site simultaneously. If the alternative sites differ sharply in quality, then individual comparisons and differences in recruitment latency should minimise the number of ants ending up in inferior nests. Sometimes, however, colony unity may only be achieved by a subsequent phase of transport from inferior sites to the best one, as we observed in colony 1. Splitting may be more common in nature than in our experiments, if the available sites are more numerous and more similar in quality than were our alternatives.

In general, why should ant colonies combine elements of distributed and individual decision-making? Recent work on foraging decisions suggests potential advantages of using a mixture of behavioural mechanisms. Ants that rely only on mass recruitment with trail pheromones are well able to settle on the better of two available food sources, but cannot always switch their efforts if a better source is discovered later (Beckers et al. 1990). Species that combine mass and group recruitment show greater flexibility in this situation. This is because a small number of group recruiters can overcome the powerful positive feedback exerted by odour trails that otherwise locks the ants into their first choice. Indeed, a similar role for small numbers of especially active or well-informed "instigators" has been proposed for the design of intelligent systems based on co-operative swarms of agents (Numaoka 1995). In general, groups may gain both greater flexibility and robustness by combining different behavioural tools to meet a given information-processing challenge.
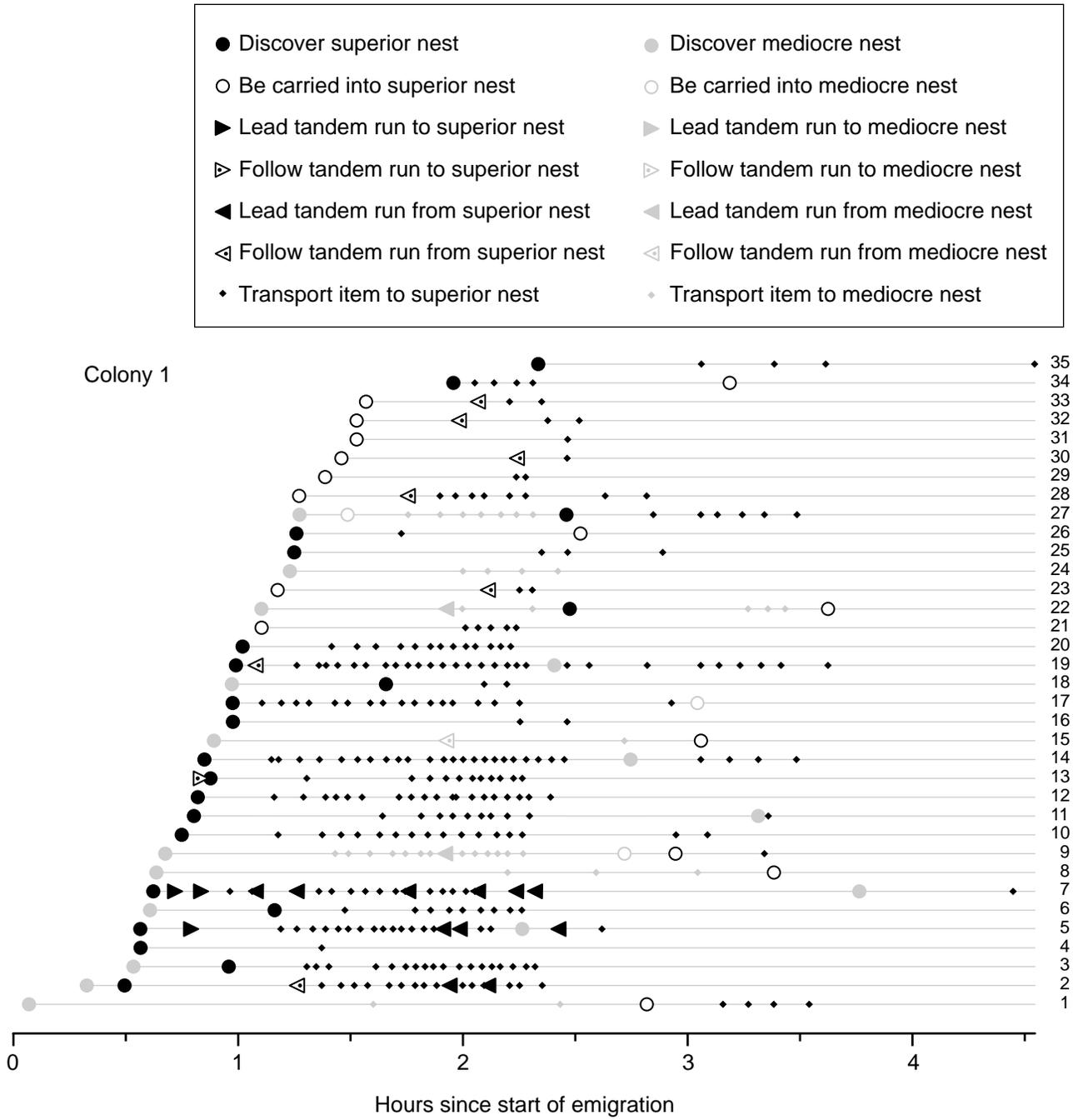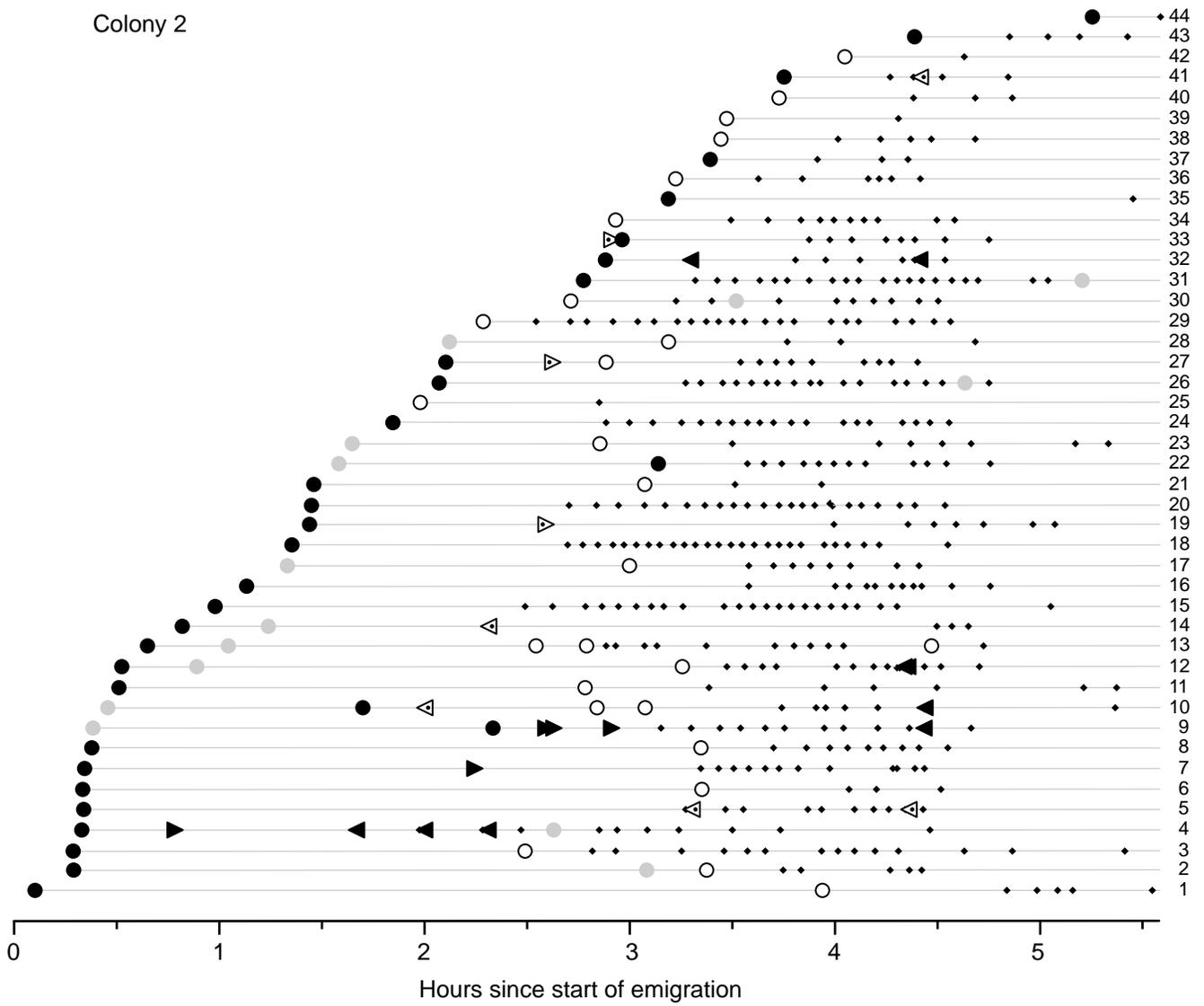
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Legend:

- ● Discover superior nest
- ○ Be carried into superior nest
- ► Lead tandem run to superior nest
- ▷ Follow tandem run to superior nest
- ◄ Lead tandem run from superior nest
- ◁ Follow tandem run from superior nest
- ◆ Transport item to superior nest
- ● Discover mediocre nest
- ○ Be carried into mediocre nest
- ► Lead tandem run to mediocre nest
- ▷ Follow tandem run to mediocre nest
- ◄ Lead tandem run from mediocre nest
- ◁ Follow tandem run from mediocre nest
- ◆ Transport item to mediocre nest

Colony 1

Hours since start of emigration

Mallon et al, Figure 2 (continued)

Colony 2

Hours since start of emigration

Colony 3

Hours since start of emigration