

Information flow, opinion polling and collective intelligence in house-hunting social insects

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The sharing and collective processing of information by certain insect societies is one of the reasons that they warrant the superlative epithet ‘super-organisms’ (Franks 1989, *Am. Sci.* 77, 138–145). We describe a detailed experimental and mathematical analysis of information exchange and decision-making in, arguably, the most difficult collective choices that social insects face: namely, house hunting by complete societies. The key issue is how can a complete colony select the single best nest-site among several alternatives? Individual scouts respond to the diverse information they have personally obtained about the quality of a potential nest-site by producing a recruitment signal. The colony then deliberates over (i.e. integrates) different incoming recruitment signals associated with different potential nest-sites to achieve a well-informed collective decision. We compare this process in honeybees and in the ant *Leptothorax albigenis*. Notwithstanding many differences—for example, honeybee colonies have 100 times more individuals than *L. albigenis* colonies—there are certain similarities in the fundamental algorithms these societies appear to employ when they are house hunting.

Scout honeybees use the full power of the waggle dance to inform their nest-mates about the distance and direction of a potential nest-site (and they indicate the quality of a nest-site indirectly through the vigour of their dance), and yet individual bees perhaps only rarely make direct comparisons of such sites. By contrast, scouts from *L. albigenis* colonies often compare nest-sites, but they cannot directly inform one another of their estimation of the quality of a potential site. Instead, they discriminate between sites by initiating recruitment sooner to better ones.

Nevertheless, both species do make use of forms of opinion polling. For example, scout bees that have formerly danced for a certain site cease such advertising and monitor the dances of others at random. That is, they act without prejudice. They neither favour nor disdain dancers that advocate the site they had formerly advertised or the alternatives. Thus, in general the bees are less well informed than they would be if they systematically monitored dances for alternative sites rather than spending their time reprocessing information they already have. However, as a result of their lack of prejudice, less time overall will be wasted in endless debate among stubborn and potentially biased bees. Among the ants, the opinions of nest-mates are also pooled effectively when scouts use a threshold population of their nest-mates present in a new nest-site as a cue to switch to more rapid recruitment. Furthermore, the ants’ reluctance to begin recruiting to poor nest-sites means that more time is available for the discovery and direct comparison of alternatives. Likewise, the retirement of honeybee scouts from dancing for a given site allows more time for other scouts to find potentially better sites. Thus, both the ants and the bees have time-lags built into their decision-making systems that should facilitate a compromise between thorough surveys for good nest-sites and relatively rapid decisions. We have also been able to show that classical mathematical models can illuminate the processes by which colonies are able to achieve decisions that are relatively swift and very well informed.

Keywords: social insects; decision-making; house hunting; mathematical models

1. INTRODUCTION

The fundamental compromise in decision-making is between speed and accuracy. The purpose of this review

is to explore solutions to this compromise in one of the most demanding and unusual examples of collective decision-making in insect societies: house hunting by complete societies. Indeed, such house hunting must be completed so quickly that effectively it is a form of crisis management. Difficult decisions, that will influence the lives of many tens, hundreds or thousands, must be made rapidly, but first much critical information must be

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One contribution of 12 to a Theme Issue ‘Information and adaptive behaviour’.

gathered and the following issues addressed. What alternative potential nest-sites are available? How do their attributes compare? Is more information needed? Which is the best course of action? This whole process is all the more demanding, not only because of the large numbers of individuals that are potentially involved, but also because there is a key requirement for consensus so that the society does not fragment. In such house hunting, indecisiveness and dissent can be deadly (Lindauer 1957). Yet, how and when does a society recognize consensus? Finally, how does it swiftly implement its collective choice?

Thus, the essential steps are these: information gathering, evaluation, deliberation, consensus building, choice and implementation. Remarkably, in both the honeybees and the ants the solutions to their house-hunting dilemmas involve both sophistication and surprising simplicity.

One of the goals of this review is to demonstrate that social insects can provide model systems for the experimental study of generic issues in information gathering, information exchange and adaptive behaviour. We have chosen to study house hunting as an example of social insect decision-making because fundamental issues are highlighted by the requirement for speed, the numbers of individuals involved and the complexity of the problem.

The processing and sharing of information pervades almost every aspect of the lives of social insects and, indeed, it is one of the reasons for their success. Social insects are extremely successful ecologically. In certain ecosystems they appear to be the dominant insects (Wilson 1990). However, for the most part they seem to have similar dietary requirements to many solitary insects. Their relatively large biomass and domination, at their size scale, in many ecosystems might then be attributable not just to the way in which they interact with other organisms but to the way in which they interact with their nest-mates, to their modifications of the environment to suit themselves and, in particular, to the efficiencies that accrue from divisions of labour (Hölldobler & Wilson 1990; Bourke & Franks 1995; Seeley 1995). Many recent studies have shown that numerous social insects exhibit a flexible division of labour that is responsive to rapidly changing circumstances in a capricious world (Tofts & Franks 1992; Bourke & Franks 1995; Beshers & Fewell 2001). This implies that social insect workers are not only engaging in useful work, but are constantly monitoring their physical and social environment for cues and signals that might indicate that they should change their occupation or intensify their activity in their current occupation. Thus, the information they receive helps individuals to decide not only what to do, but also how, where and when to do it. Hence, the management of information flow can be regarded as crucial to the success of insect societies (Detrain *et al.* 1999a; Franks 1999; Camazine *et al.* 2001).

Careful monitoring and rapid response to information is probably crucial in all the decision-making that occurs within social insect colonies. Moreover, house hunting is arguably an especially illuminating case because it involves just such adaptive decision-making, both at the individual and at the collective level and it requires the choice of a single course of action.

In our own families and societies house hunting and home relocation are popularly considered to be one of the

events most likely to cause distress (Holmes & Rahe 1967; Brown 1989; Wethington 2000). The choice of a new home is a massively costly decision that must be made relatively quickly, yet it is likely to be binding for a considerable period in the life of the occupants. Part of the anguish of house hunting can be attributed to the cascade of difficult decisions that must be made, and to the large amounts of disparate information that must be collected and evaluated at each decision point. These difficulties are exacerbated because the required information is likely to be, in part, erroneous and outdated rather than accurate and timely. Overarching all of these issues is the additional problem of the speed of decision-making—when should a family reject an adequate new home to continue to search for a better one, given that the result might be additional costs or even homelessness?

These massive challenges must be faced during house hunting, not only by ourselves but also by social insects. However, the problems that must be solved seem to be of an even greater magnitude for certain insect societies. Many tens, hundreds or tens of thousands of individuals may need to take up a new residence together. Hence, their homes are often massive compared with the size of the individual organisms that will initially survey them. The discovery of potential nest-sites and their surveys are likely to be time-consuming, error-prone and potentially dangerous and so only a very small minority of the colony's total population may have the opportunity, directly, to compare alternative nest-sites for themselves. This, in turn, means that social insect colonies may need to compare the estimated value of alternative sites by evaluating the information returned by large numbers of different scouts over a relatively protracted period. Given all of these difficulties, it seems probable that a colony will receive conflicting information from different scouts (unless natural selection has endowed scouts with super-accuracy in their evaluation and reporting of potential nest-sites). For example, some may consider that a certain nest-site is rather poor while others may rate it as excellent. Hence, there are also issues of statistical sampling and opinion polling. Only then may a colony attempt to achieve a colony-wide consensus over the best available nest-site and finally instigate a lock, stock and barrel emigration to their chosen new home.

This review will compare such house hunting in honeybees (*Apis mellifera*) and in one species of ant (*Leptothorax albigipennis*). These are the only two cases in social insects that have been studied in any detail (for such studies of bees see Lindauer 1955, 1961; Seeley 1982; Seeley & Buhrman 1999, 2001; Camazine *et al.* 1999; Visscher and Camazine 1999a,b; Visscher *et al.* 1999; Seeley & Tautz 2001; and for such studies of ants see Mallon & Franks 2000; Mallon *et al.* 2001; Mugford *et al.* 2002; Pratt & Pierce 2001; Pratt *et al.* 2002). We believe that the comparison of house hunting by honeybees and *L. albigipennis* is both attractive and illuminating. This is because there are many similarities, as listed above, in the issues they face, and there are both similarities and differences in the way in which they solve these problems. We will begin to illustrate this in the next section of this review by examining the natural history of house hunting in honeybees and *L. albigipennis*. We will then review experiments that show how key information is collected and decisions are made,

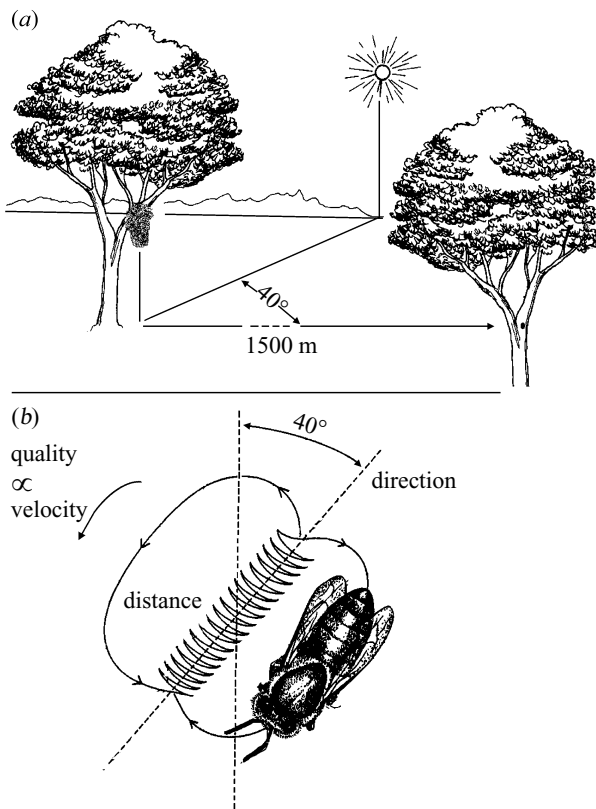


Figure 1. Recruitment via the waggle dance of the honeybee. (a) A scout from a swarm in the tree on the left has found a potential new nest-site in another tree 1500 m away and 40° clockwise of the sun. (b) The bee can indicate the direction of the new nest encoded in the angle of her waggle run, the distance in the duration of the straight waggle run and the quality in the speed with which she repeats the waggle run. Modified from an illustration of nectar foraging by honeybees in Seeley (1985), fig. 7.1 and used with the kind permission of Tom Seeley and Princeton University Press.

both at the individual and at the collective level. Then we will compare and evaluate mathematical models of these decision-making processes. Finally, we will summarize the major insights that arise from both the empirical and modelling studies.

2. THE NATURAL HISTORY OF HOUSE HUNTING IN HONEYBEES

House hunting in honeybees is typically associated with colony propagation. In the late spring, large colonies rear a small number of new queens, one of which will eventually inherit the portion of the colony that stays in the old nest. Even before these new queens have completed their development, the old mother queen and roughly half of the colony's workforce move out of the old nest. The old queen and her 15 000 or so loyal workers thus set out, but typically initially travel less than 100 m, where they all alight in a beard-like swarm on a structure such as the branch of a tree. Almost immediately, scouts fly off in all directions from the swarm to seek suitable new nest-sites—cavities in trees and buildings—and some may travel more than 10 km from the swarm in their determined search for a new home (figure 1a). The scouts are, in general, middle-aged bees with foraging or flight experience,

and are perhaps the bees most likely to be familiar with the landscape around the swarm (Gilley 1998). However, a surprisingly small number of scouts may take an active role in house hunting; they may number from tens to a few hundred bees and are thus, at most, only *ca.* 5% of the total population of the swarm (Seeley 1982).

Tom Seeley and colleagues (Seeley 1977, 1982; Seeley & Morse 1978; Visscher *et al.* 1985) have shown, for bees in upstate New York, that scouts assess a whole series of variables when they encounter a potential nest-site. These include: (i) the volume of the cavity—they reject cavities above 100 l and below 10 l; (ii) the size of the entrance; (iii) the height of the entrance above the ground; (iv) the height of the entrance above the floor of the cavity; and (v) the compass bearing of the entrance. These variables are of adaptive significance because they will determine if there is room for the colony to grow in the new cavity and store sufficient honey for over-wintering, and how well the cavity can be defended and maintained at a certain temperature. To investigate how scouts assess some of these variables, Seeley conducted further experimental work on Appledore Island off the coast of Maine. This island has no large hollow trees that could provide distracting natural nest-sites. Seeley could then supply carefully controlled experimental nest-sites to small experimental swarms of some 2000 bees. These observation nest-boxes were attached to the side of a hut with a red window forming the party wall between the scout bees inside the chamber and the observer in the hut. A scout bee needs *ca.* 40 min, initially, to inspect a nest-site. During this discovery phase, it enters the nest-site for many short visits punctuated with sojourns outside. After this phase a scout may revisit a good site but such visits become more and more sporadic and cursory with increasingly long periods, extending to approximately an hour, or more, spent away from the site. This suggests that the scout makes most of her assessment of a new nest-site during the discovery phase and spends most of the rest of the time back with the swarm. Experiments with a cylindrical nest-site on a turntable show, for example, that scouts assess the volume of the cavity by walking its inside surface (Seeley 1977, 1982). Nevertheless, how they translate such measurements into an assessment of cavity volume, and how they measure the other variables that concern them, is unknown.

It is clear from the observations and experiments of Lindauer (1955, 1961) and Seeley & Buhrman (2001) that scouts advertise the charms of potentially suitable nest-sites by dancing more or less vigorously on the surface of the swarm (figure 1b). From these dances, other scouts can read the distance and direction of potential nest-sites and may then visit such nest-sites themselves and also, in turn, dance more or less ardently to indicate their enthusiasm for a certain site. Currently, there is no evidence that bees monitoring dances obtain information about nest-site quality, but nest quality is indirectly indicated by the vigour of a dance (T. D. Seeley, personal communication). Longer dances for better sites will gather more recruits.

After an extended period of deliberation, in which many scouts may dance for many potential sites, a consensus is achieved in which only one nest-site is danced for vigorously. At this point, the swarm becomes primed and prepares itself for flight. First, approximately an hour before

take-off, the swarm heats up to *ca.* 35 °C, the optimum temperature for the flight muscles (Heinrich 1981). This warming up is evidently triggered by distinctive piping sounds emitted by nest-site scouts and perhaps other bees (Seeley & Tautz 2001). Then the scouts, now almost perfectly unified in their choice of a new nest-site, pierce the swarm with buzzing runs, literally stirring it up for action by barging and boring their way through clusters of their nest-mates while periodically buzzing their wings. An intense humming noise, an insistent combination of buzzing and strident piping, both percolates and is broadcast from the swarm. The intensity of this signal reaches a crescendo just as the once-cohesive cluster of bees begins to dissolve into a dripping emulsion of extremely excited bees. The entire swarm becomes airborne. It forms a missile, of myriad components, in a formation 10 m in diameter. The swarm super-squadron accelerates to 3 m s⁻¹ and streaks across the sky towards the new nest-site, which may be several kilometres distant. The scouts may even help to orientate the swarm in flight by firing themselves through the swarm in the direction of the chosen home-stead. For a detailed description of the natural history of the flight of honeybee swarms see Seeley *et al.* (1979).

The scouts alight at the entrance to the new nest-site and release assembly pheromone from the Nassanoff gland in the distal region of their abdomen, whereupon the other bees land and crawl through the entrance to their new home. The entire emigration from the original swarm-site into the new hive only takes *ca.* 30 min and immediately all of the work of setting up the new home begins.

3. THE NATURAL HISTORY OF HOUSE HUNTING IN *LEPTOTHORAX ALBIPENNIS*

Franks and his colleagues specially selected *L. albipennis* for intense study because it naturally lives in very small colonies in thin cracks in rocks (Franks *et al.* 1992; Franks & Sendova-Franks 1992; Sendova-Franks & Franks 1993). For this reason, colonies can be cultured in the laboratory in nests made from microscope slides that mimic the dimensions of natural nest-sites. This, coupled with the relatively small worker populations of established colonies, which are often just 100 strong, means that all of the workers can be individually marked with identifying paint and all of them can be constantly observed.

In nature, there is evidence that colonies can build a protective wall around themselves within the existing rock cavity they inhabit (Franks *et al.* 1992; Franks & Deneubourg 1997). The fissure in the rock provides both the floor and the roof of their nest, separated by a gap of only *ca.* 1 mm. Colonies are collected on scree slopes, or in old Portland stone quarries, on the English Channel coast of Dorset. Even though colonies can build simple dry-stone walls they cannot build a roof to their nests. The cavities they inhabit are in friable rock slivers (i.e. in rocks that break up under weathering) and it is likely that existing nests often become uninhabitable due to mechanical disturbance or even flooding. Thus, house hunting in *L. albipennis* may often occur when established colonies need to find a new home because their old one has been damaged beyond repair. *Leptothorax albipennis* appears to

be seasonally polydomous—at certain times of year colonies split to occupy multiple neighbouring sites (Partridge *et al.* 1997). Why they do this is, as yet, unknown. However, for the rest of the year it seems likely that an emigrating colony would gain by choosing only one new nest-site. In the field, neighbouring colonies are often found less than 30 cm apart, and it seems very likely that a colony would emigrate only a few centimetres to a new nest-site if one were available. In other words, colony emigration is not necessarily associated with colony propagation or with dispersal in this species. Rather, it is a response to the emergency of the old nest being no longer habitable.

In contrast to house-hunting honeybees that may examine an area of 150 km² (Camazine *et al.* 1999) in the search for a new nest-site, *L. albipennis* may examine an area of only 1 or 2 m² (N. R. Franks, personal observation). The bees can fly at 3 m s⁻¹ but must survey a huge area for very few nest-sites, which they can only discover by looking for small potential entrance holes (imagine having to examine every knothole in a huge forest in case it is a portal to a suitable cavity). The survey procedure for the ants is thus, arguably, much easier. They travel much more slowly, only *ca.* 5 mm s⁻¹ but, comparatively, they have a much smaller area to examine than the honeybees, and potential nest-sites may be relatively more common. This difference probably means that many more ants than bees make individual discoveries of potential nest-sites and may even stumble upon more than one.

The very small size of *L. albipennis* colonies and the small size of their workers (each *ca.* 2.5 mm long) make it very difficult to study their behaviour in the field. However, their tiny size means that emigrations can be staged, at a natural scale, on the laboratory bench and both the old and new nest-sites and all traffic in between can be readily observed and videotaped (Sendova-Franks & Franks 1995; Franks & Sendova-Franks 2000).

In the laboratory, colonies can be induced to find a new house simply by removing the top microscope slide from their old nest. They can then be presented with a choice between two or more potential nest-sites and their preferences can be determined by recording, in carefully replicated experiments, which nest-sites they most often choose to colonize. Although laboratory colonies habituate easily to living in transparent well-illuminated nests, which facilitate filming, experiments show that they do prefer dark nests to light ones. They also prefer a narrow nest entrance (1 mm is preferred to 4 mm, for example) and a relatively high cavity ceiling (1.6 mm of headroom is preferred to 0.8 mm) (Mallon *et al.* 2001; Franks *et al.* 2003).

All of these factors are probably relatively easy for a single scout to assess. It might, for example, measure the width of the nest entrance by stretching wide its antennae, and it might judge the internal height of the nest cavity by raising its antennae from the floor to the ceiling. It is probable that these ants prefer such nest dimensions as a compromise between having, on the one hand, enough space both to enable the relatively large queen to enter the nest cavity and to tend large brood items, and, on the other hand, gaps that are sufficiently narrow to prevent larger ants and other predators from entering their nest and stealing their brood.

Experiments also show that individual scouts can measure the floor area of nest-sites before selecting them. This is a far more difficult problem. First, nest floor areas are large compared with the size of an individual ant. The small laboratory nests that we use as standard have a floor measuring 35 mm × 23 mm and are thus about 10 times longer in both of these dimensions, than the body length of individual workers. More remarkably, however, individual scouts, given the choice, can reliably reject nests that are only three-eighths smaller than standard sized nests (Mallon & Franks 2000).

How these ants assess the floor area of potential nests has been the subject of a series of experiments (Mallon & Franks 2000; Mugford *et al.* 2002). There is good evidence that scout ants make multiple visits to potential nest-sites. The experimental procedures involved videotaping colonies in which all of the workers had been uniquely identified with paint dots, substituting new nest-sites between first and second visits and even quickly removing parts of false floors between visits. From such experiments the following evidence has been amassed. On their first visit scouts deploy individual-specific trail pheromones as they meander across the floor of the cavity. They then leave the nest and on their second visit assess the frequency at which they cross their previous path. This could provide a reasonably reliable index of the size of the floor area irrespective of the shape of the nest. For example, the larger the floor area the lower will be the frequency at which an ant will cross its first-visit path during its second visit. It seems crucial that the trail pheromones are specific to individuals to ensure that path-crossing frequencies provide a reliable index of floor area. If all scouts used identical trail pheromones then trail-crossing frequencies would depend on the indeterminate numbers of scouts that had visited a nest-site and not just its floor area.

When an individual scout has determined, to her satisfaction, that a new nest-site is suitable, she begins to recruit her nest-mates one at a time to the new nest-site. Such scouts may use their own individual-specific trail pheromones to help them find their way to and from the old and new nest-sites, but in *Leptothorax* such pheromones are not used for recruitment (Maschwitz *et al.* 1986; Aron *et al.* 1988). Rather, the scout begins to recruit nest-mates by taking them on a tandem run all the way to the new nest-site (figure 2*a*). A tandem run involves the scout finding a receptive ant at the old nest-site and leading it physically. The ant at the rear follows its leader in a close-coupled march during which it taps very frequently, with its antennae, the abdomen of its guide. Such tapping informs the leading ant that it has not lost its disciple. Tandem running is slow, however, because leader and follower briefly but often part company and the leader must wait for its follower to catch it up. Tandem running has an average velocity of *ca.* 1.5 mm s⁻¹ (Pratt *et al.* 2002). However, one benefit of tandem running over the faster recruitment by carrying that occurs later (figure 2*b*), is that the ant being led adopts the same position as it would if it were finding its own way. This may enable her both to deposit her own orientation pheromones and to learn the visual landmarks known to be used for orientation by recruiters between nest-sites during emigrations (Pratt *et al.* 2001;

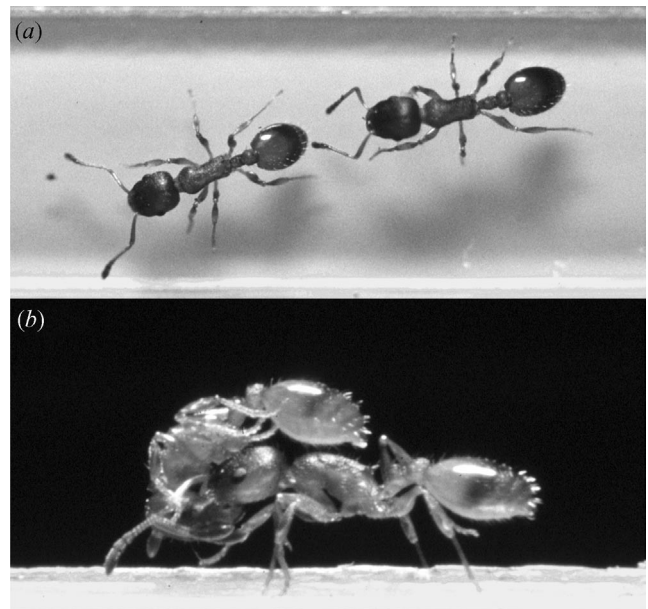


Figure 2. (a) Recruitment via tandem running in the ant *Leptothorax albipennis*. The worker at the front is leading the tandem run, and the follower behind is about to signal its presence by tapping with its antennae on the gaster of the leader. (b) Recruitment by transport in *L. albipennis*. One worker is simply carrying another quickly to the new nest-site. (Both photographs by S. C. Pratt.)

McLeman *et al.* 2002). Möglich (1978) has referred to tandem running in *Leptothorax* as 'the recruitment of recruiters'. Indeed, in house-hunting *L. albipennis*, tandem run followers are disproportionately likely to become recruiters (Pratt *et al.* 2002). Later, faster recruitment by carrying feeds forwards into a full emigration, with a rapid growth of the population in the new nest as more and more individuals, the queen, the workers and their brood (eggs, larvae and pupae), are shuttled across to their new abode. Carrying recruitment has an average velocity of *ca.* 4.6 mm s⁻¹ (Pratt *et al.* 2002).

In stark contrast to honeybees, *L. albipennis* do not have a communication behaviour, such as the waggle dance, to encode their enthusiasm for a nest-site on a continuous sliding scale from less vigorous (moderate enthusiasm) to more vigorous (extreme enthusiasm). However, the switch from slow tandem running to the faster carrying of nest-mates may represent an important step change in the rate of the recruitment process (see later). Furthermore, in contrast to the waggle dance of the honeybees, these ants do not have a system of group recruitment in which one scout can, at least potentially, simultaneously inform many others of the whereabouts of a good site.

Occasionally, a colony presented with an acceptable new nest and a better one may begin recruitment to each more or less simultaneously. In these cases, a minority of ants and brood may be brought to the inferior site, requiring a second stage of emigration to usher them to the better site. However, in the majority of cases, colonies can move directly to the better site in a single phase.

We will now review experiments that explore how these decisions in favour of the best nest-sites are made, first in the honeybees and second in the ants.

4. EXPERIMENTAL INVESTIGATIONS OF THE DECISION-MAKING PROCESS: THE BEHAVIOUR OF SCOUTS AND COLONY-LEVEL RESPONSES

There are both major similarities and major differences in the house-hunting procedures of honeybees and *L. albipennis*. The most important similarities are: (i) both kinds of colony are able to select the best among many alternative nests each with many attributes; (ii) the assessment of nest-sites is made by individual scouts working alone; (iii) the majority of scouts do not directly compare different nest-sites by visiting and ranking them (see below); (iv) scouts translate their evaluation of nest-sites into recruitment signals and (v) (as a consequence of points i–iv) at least part of the choice procedure involves a process of deliberation in which the information coming back to the colony from different scouts is in some way compared, evaluated and consolidated.

We believe that these similarities are of great importance. What makes them even more noteworthy is that they are exhibited as a complete syndrome by otherwise very different types of social insect. For example, the honeybee swarm is two orders of magnitude larger than colonies of *Leptothorax* in terms of numbers of individuals (*ca.* 10 000 versus 100). There are also, of course, a number of fundamental differences in their recruitment systems. The honeybees utilize their famous waggle dance during house hunting—a system of group recruitment in which a single scout bee can, at least potentially, inform many others concurrently about the distance and direction of a new nest-site (or a patch of flowers). The *Leptothorax* ants, by contrast, do not even use recruitment trails, but simply lead or carry nest-mates, one by one, to a new nest-site (or patch of food). Thus, these ants not only have one-by-one recruitment but they also seem to have little or no opportunity to modulate their recruitment signals to encode the quality of a nest-site. Their simple recruitment has a binary, all-or-nothing, form.

Therefore, the issue here is this: given all of these differences and apparent deficiencies, how can *L. albipennis* colonies match, as they do, the decision-making abilities of honeybee colonies? We will seek answers to this question first in the behaviour of the scouts of both types of colony. Thus, in this section of this review we will examine recent experimental evidence that shows how the behaviour of individual scouts feeds forward into the decision-making of their colony.

(a) *The behaviour of house-hunting honeybee scouts*

There have been two independent and recent sets of studies of house-hunting honeybee scouts: one by Seeley & Buhrman (1999, 2001) and the other by Visscher and Camazine and their colleagues (Visscher & Camazine 1999a,b; Camazine *et al.* 1999). The basic procedure was to mark all of the honeybees individually in relatively small observation swarms that have been taken to sites (such as a small offshore island or a desert environment) in which swarms could be presented with choices among controlled, artificial nest-sites. The experimenters then recorded which scouts visited which sites and videotaped all of the dancing of house-hunting scouts on the surface of the swarms. A human observer can determine, by watching such dances, the distance and direction of a nest-

site and in this way determine which nest-sites each dancer is advertising. Hence, a picture can be built up of all of the behaviours, through time, of all the scouts from the moment house hunting begins to the moment the swarm takes off to fly to its chosen new home. One such time-line study is shown in figure 3a.

The most important findings, from both sets of researchers, are as follows.

- (i) Individual scouts may initially dance for any site they have encountered that they consider to be above some threshold of acceptability.
- (ii) Dances associated with house hunting can be unusually long and vigorous (compared, for example, with dances advertising sources of pollen or nectar).
- (iii) Dancers encode the direction of the nest-site they have found in the angle of their waggle runs. They indicate the distance by the duration of their waggle runs, and they indicate quality by how rapidly they execute the return phase of the dance, as well as by the overall duration of each bout of dancing (Seeley & Buhrman 2001).
- (iv) Between dances, scouts may revisit the nest-site they have been advertising. Scouts may monitor dances for alternative sites.
- (v) Many scouts cease dancing each day.
- (vi) A small (and possibly important) minority of scouts may switch their allegiance from one site to another and visit and dance for that alternative site.
- (vii) The colony-level consensus over nest-site choice is built principally from two processes: (i) scouts dropping out of dancing for less favourable sites (without actively switching to new sites); and (ii) more and more new scouts being recruited to, and dancing for, the best site.

Seeley *et al.* (1979) estimated that *ca.* 5% of the bees in a swarm actively look for nest-sites, but only about one third of the scouts that visit a site advertise it by dancing (see Camazine *et al.* 1999). Dances for nest-sites were nearly twice as long as those advertising nectar and pollen (Camazine *et al.* 1999). When a scout ceases dancing, she may monitor dances by other scouts for the site she had previously advertised, or for other sites. However, such scouts appear to do so indiscriminately (*i.e.* at random). In one swarm, studied by Visscher & Camazine (1999b), of the 46 (formerly dancing) scouts that monitored dances no later than 30 min before swarm take-off (and thus had good opportunity to examine the dances of other bees), 41% monitored dances for the same nest-site that they themselves had danced for, 13% monitored dances for the alternative site, and 35% monitored dances for both sites (the remaining 11% did not monitor other dances during this period). These frequencies are similar to those expected if scouts simply monitored dances at random, *i.e.* in proportion to their occurrence on the swarm (Visscher & Camazine 1999a). However, this analysis arguably provides only weak evidence against non-random dance following, because the two potential nest-sites in this experiment were identical (T. D. Seeley, personal communication). Scouts that monitor dances for different sites may visit more than one site, but this appears to be

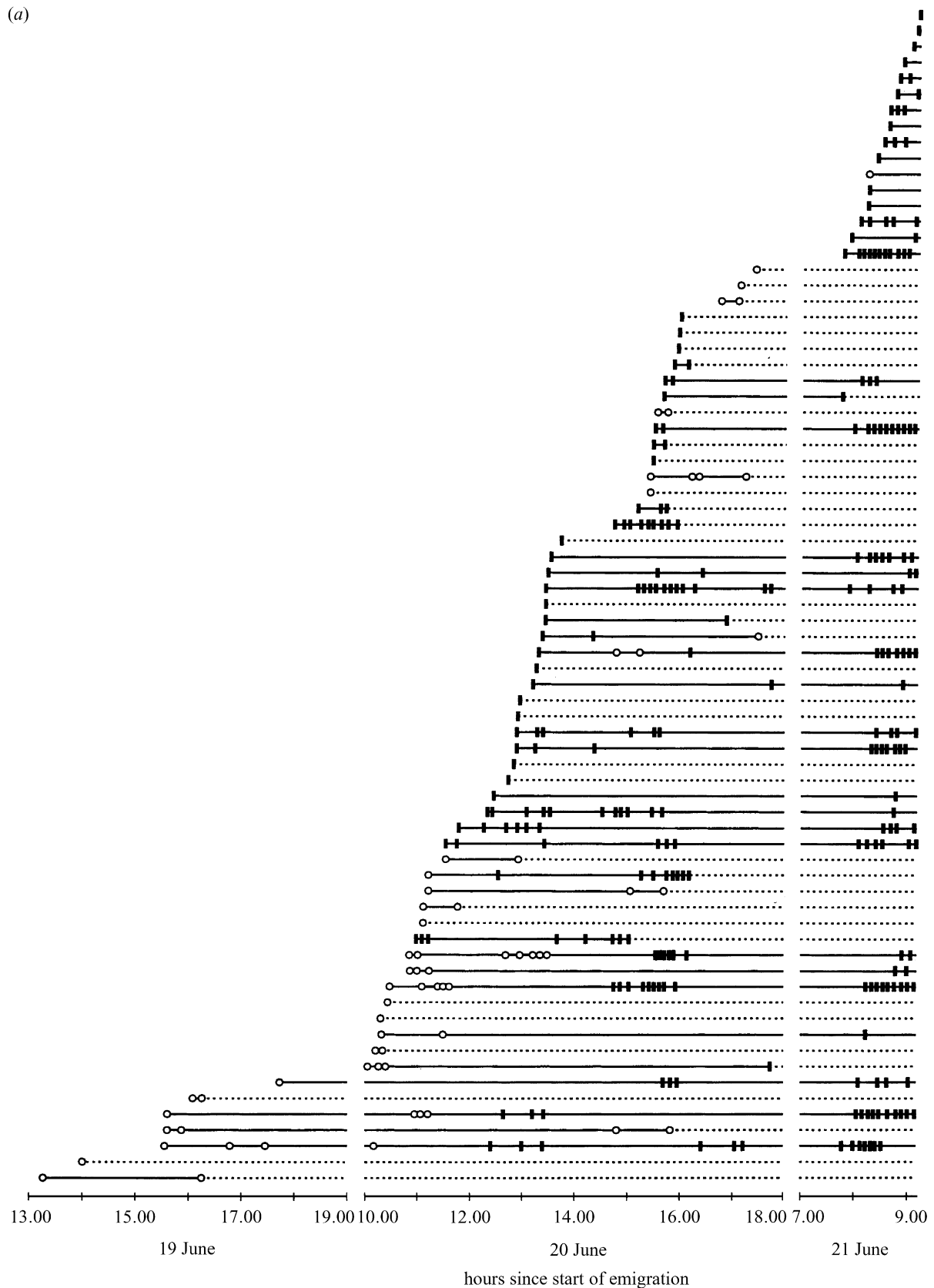


Figure 3. (Caption overleaf.)

quite rare. Only between 5 and 10% of the scout bees studied by Camazine *et al.* (1999) visited both of the potential new nest-sites available to the swarm. In the experiments of Camazine *et al.* (1999), 9.2% of all scouts (16 out of 174) visited both of the two available sites: 11

of these (6.3%) first visited the inferior site and then visited the better site only later in the process, when nearly all dancing was for the better site. Only five scouts (2.9%) first visited the better site, and then later visited the inferior site. Even though very few bees are involved in

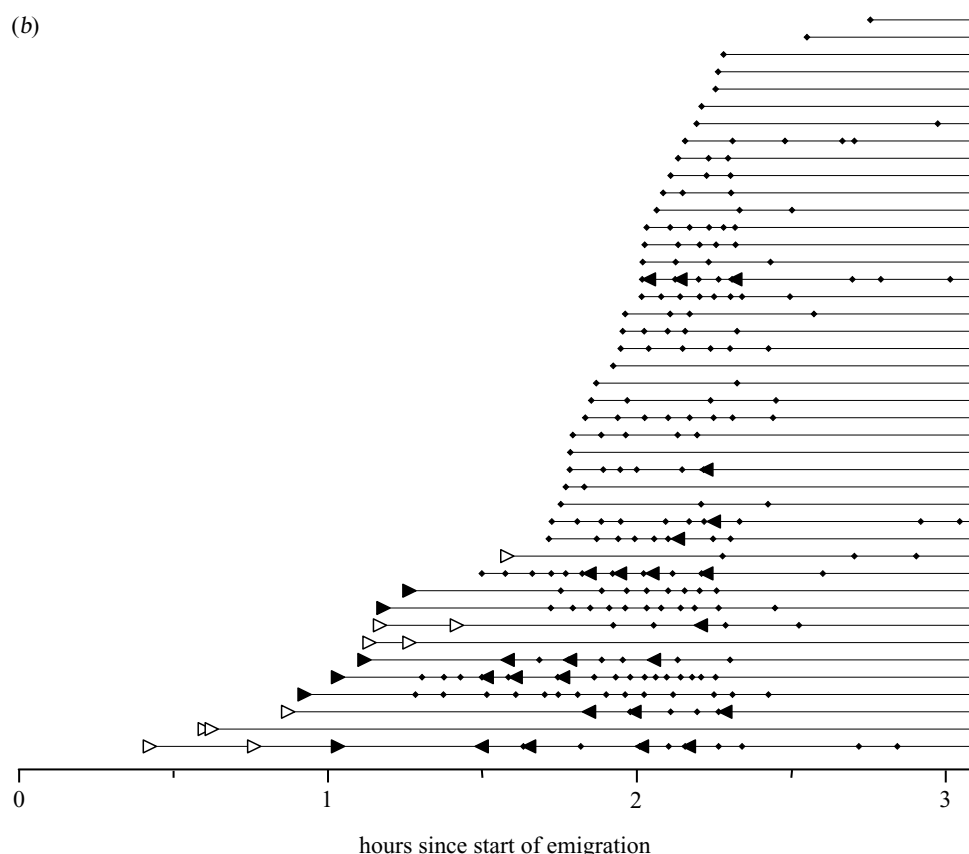


Figure 3. (a) Time-line records of the dancing by each of 73 scout bees that performed dances in one swarm studied by Seeley & Buhrman (1999). An open circle denotes a dance for a non-chosen site, whereas a black bar denotes a dance for the chosen site. A dashed horizontal line indicates when a bee has ceased and does not resume dancing before the swarm departs to its chosen nest-site. The three days over which the swarm deliberated are shown with the bottom line in the stack of time-lines representing the first scout to dance and the top line the last. Reproduced with kind permission from Tom Seeley and Springer-Verlag. (See Seeley & Buhrman 1999 for further details.) (b) Time-lines for the behaviour of ants actively involved in recruitment during nest-site choice by a colony of *Leptothorax albigipennis*. Key: filled triangle pointing to the right, led tandem run from old nest to superior new nest; filled triangle pointing to the left, lead tandem run from superior new nest to old nest; empty triangle pointing to the right, lead tandem run from old nest to mediocre new nest; empty triangle pointing to the left, lead tandem run from mediocre new nest to old nest; filled small diamond, transport item from old nest to superior nest (no transports to mediocre nest in this emigration). The three hours from the start of the emigration are shown with the bottom line in the stack of time-lines representing the first ant to recruit and the top line the last. (See Mallon *et al.* (2001) for more details.)

direct comparison of nest-sites, it might be argued that these cognoscenti wield a disproportionate influence. However, evidence that direct comparison of different nest-sites by individual scouts is unlikely to be important comes from experiments by Visscher & Camazine (1999a), in which scouts that were seen to visit two sites were immediately captured and prevented from taking any further part in the process. The removal of such individually well-informed scouts did not seem to arrest the decision-making process in any significant way. However, these experiments may underestimate the importance of direct comparison because both of the potential nest-sites were excellent ones. If they had differed in quality it is possible that Visscher & Camazine (1999a) may have seen an effect of their manipulation (T. D. Seeley, personal communication). Nevertheless, it seems clear that the final consensus does not *require* honeybees to compare nest-sites directly. Nor do the bees appear to rely on indirect comparison of sites, for example, by comparing their own enthusiasm for a site with that encoded in dances for other sites. Instead, individual scouts simply withdraw from the

process by ceasing to dance after a while (see Lindauer 1955; Seeley & Buhrman 1999). In this way, the decision is handed over, progressively, to cohorts of naive or refreshed bees that can make unprejudiced decisions to visit those sites that are most enthusiastically advertised at the time that they first start, or start once again, to monitor dances. These bees may then decide to advertise sites themselves, and they also may continue, or cease, dancing before the swarm takes off.

Therefore, to summarize, two counteracting processes seem to be sufficient for a consensus to emerge: first, the strong positive feedback of vigorous and enthusiastic dancing for good sites which attracts more and more dancing for such sites, and second, the restraining, attritional process of individual bees ceasing to dance.

However, certain mysteries still remain about honeybee house hunting. One prominent mystery is how the process comes to an end. Although many authors have used the term unanimity to describe the end of the decision-making process, this is an inappropriate term. Unanimity means by general consent and therefore implies that all the

individuals involved agree. This, in turn, implies that they all have access to the crucial information upon which to agree. This is not the case. Even at take-off a few bees may still be dancing for alternative sites (Seeley & Buhrman 1999; Camazine *et al.* 1999), and the vast majority of bees in the swarm have received no information at all. They merely defer to a decision made by others. Given this lack of true unanimity, what signals the end of the process of deliberation? Camazine *et al.* (1999) have speculated that scout bees may decide that sufficient consideration has been given to a nest-site on the basis of the number of scouts present at that site. In other words, a crucial aspect of collective decision-making may occur not in the swarm, but at the nest-site, where scouts decide to activate the swarm once a threshold density of scouts has been surpassed. If so, this process would be analogous to the recently demonstrated head counting that determines the switch from slow to fast recruitment in *L. albipennis* (Pratt *et al.* 2002 and see below). In both cases, scouts need not actually count heads, but may instead assess encounter rates or even the concentration of chemical cues or signals produced by nest-mates at the site.

A second major remaining mystery is this: how does the swarm as a whole know where to find the new nest-site given that, at take-off, only a tiny proportion of the bees have visited it or monitored dances advertising the chosen site? As mentioned above, scouts might possibly influence the direction taken by the swarm by flying through it. For the ants, the simplicity of a decision-making system in which nest-mates are led or carried, one by one, to the new nest-site solves the problem of informing the colony as a whole about the new nest-site's location.

(b) *The behaviour of house-hunting scouts of Leptothorax albipennis*

Mallon *et al.* (2001) and Pratt *et al.* (2002) have conducted studies of the behaviour of individual scouts during house hunting by colonies of *L. albipennis*. As in the studies of the honeybees, all of the workers in the study colonies were uniquely marked so that they could be recognized, and the behaviour of all the scouts, from the moment the old nest was destroyed until the end of the emigration to the new nest, was recorded using video cameras. Figure 3b shows the time-lines for the scouts in one colony.

Therefore, the findings can be summarized as follows.

- (i) In choices between two nests, many scouts visit both nest-sites, compare them, and choose the better one.
- (ii) Nearly half of the scouts, however, encounter only one nest in the course of an emigration.
- (iii) These poorly informed ants also contribute to the colony's decision, because their probability of initiating recruitment to a site depends on the site's quality.
- (iv) This means that scouts at a superior site have *shorter latencies* between their first entry at the site and their first recruitment to it, thus driving up the better site's population more rapidly than that of an inferior site.
- (v) This difference is enhanced by the ants' reliance on two distinct forms of recruitment: (i) at first, they summon fellow recruiters via tandem runs, in which

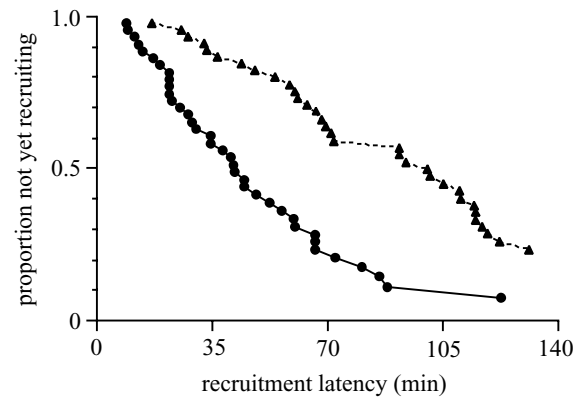


Figure 4. The number of ants not yet recruiting as a function of time since each ant first entered the nest-site. Ants at a mediocre site are indicated by triangles and those at a superior site by circles. Analysis of such 'survivorship curves' shows that individual ants hesitate for less time before recruiting to a superior site than they do for a mediocre one. (See Mallon *et al.* (2001) for further details.)

a single follower is physically led all the way to the new site; (ii) they later switch to recruiting the passive majority of the colony via transports, a speedier method in which nest-mates are simply carried to the site.

- (vi) 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 nest-mates is present.
- (vii) The quorum requirement amplifies the difference in recruitment speed between better and worse sites, by making the launch of rapid transport dependent on convincing enough active ants of the worth of the site.

One of the key factors in this scenario is the recruitment latency time. Figure 4 shows that the probability of a scout beginning to recruit to a new nest is largely independent of time for a particular nest but is higher for a nest of higher quality. Unlike the honeybees, these ants cannot encode, on a continuous sliding scale, their enthusiasm for a particular nest-site in the vigour of a dance, nor can they, like some ants recruiting to valuable food sources, encode the perceived value of a resource in the amount of recruitment trail pheromones they deposit (see Detrain *et al.* 1999b, for a review). The act of recruitment in *L. albipennis* seems to be, for the most part, a simple binary on/off signal 'Follow me!' (figure 2a) or 'Let me carry you!' (figure 2b). However, the crucial sliding-scale representation of nest-site quality is reflected, in part, in the speed at which a scout is prepared to begin recruiting its nest-mates. This is a remarkably beautiful mechanism. Doubtless, procrastination is the thief of time, but here such procrastination is a vital ingredient in the rejection of poorer nest-sites. This is likely to be a particularly adaptive mechanism because it can be both forgiving and self-correcting. For example, if a scout slowly recruits another potential scout to an acceptable but not outstanding nest-site, that second scout is also likely to be slow to recruit others. Hence, the other ants in the colony have the time to find and to begin to recruit their nest-mates more

swiftly to a better site. This mechanism can be self-correcting because if, owing to examination errors, a scout has a low opinion of what is actually a very good nest-site to which it slowly recruits others, these secondary scouts can form their own opinions and can begin swiftly to recruit to that site. In such a way, initially erroneous decisions can be overridden.

Although both forms of recruitment in *L. albipennis* are all-or-nothing in form, the ants may gain extra control in the decision-making process from the slower speed of tandem running, used immediately after a nest has been discovered, compared with the fast-carrying recruitment used later. The use of slow tandem running may be crucial. It may provide more time for alternative and better sites to be discovered by supplementing the latency period preceding recruitment. The ants that have been led by a tandem run to a new nest-site, after they have completed their own assessment of the site, may in turn slowly lead recruits there. This positive feedback slowly drives up the number of visitors to the site. If separate groups of ants independently discover two sites of different quality, such feedback favours the better site, because the length of the assessment stage varies inversely with site quality. Another crucial stage in this process is the switch from slow tandem-running recruitment to fast-carrying recruitment. Recent work by Pratt *et al.* (2002) has shown that the switch between these behaviours depends on the number of ants at the new site. Experimentally transferring ants from the old nest to the new site, so that the first independent discoverers find the new site already crowded with nest-mates, inhibits tandem runs in favour of transports. Conversely, the tandem-run phase can be greatly extended by experimentally preventing the increase in site population that is normally caused by tandem runs. Thus, recruiters appear to switch from tandem runs to transport only when the new site's population has crossed a threshold (figure 5). Such a threshold is analogous to an opinion poll / voting procedure. The more nest-mates that are present in a new nest-site, the more certain an ant can be that a good number of its nest-mates also consider that it is a suitable new home. Thus, once the number of visitors has surpassed a threshold, the ants enter the final stage of decision-making, switching to a more rapid form of recruitment in which they carry the bulk of the colony from the old nest. The population dependence of this switch also ensures an adequate corps of transporters for efficient relocation of the colony. More importantly, it may sharpen the precision of both individual and collective decision-making. At the individual level, the threshold allows each ant to supplement her own appraisal of the site with an indirect cue about the evaluations of other ants. At the colony level, quality-dependent assessment durations cause better nests to reach the threshold sooner. The subsequent acceleration of recruitment further amplifies the better site's advantage over inferior alternatives.

After the switch, workers sometimes lead tandem runs in the opposite direction, from the new nest back to the old (figure 3*b*). The function of these reverse tandems remains unclear, but one possibility is that they summon ants to help retrieve nest-mates from the old site. This switch in the direction of tandem running may indicate that even before the emigration is complete, many ants

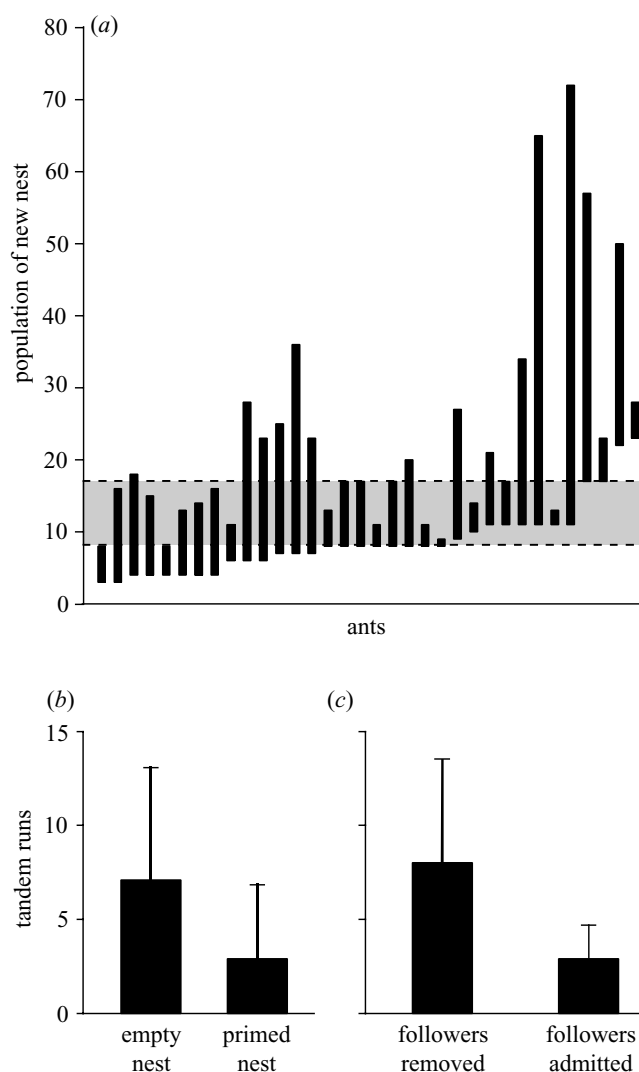


Figure 5. Recruiting ants use tandem runs when the population of their nestmates at a new nest-site is small and they use transport when it is high. (a) Estimate of nest-site population at which ants switch from tandem running to transport. The ends of each black bar show the upper and lower bounds of the estimate for a single recruiter. The upper and lower margins of the grey zone show the median upper and lower bounds, respectively. (b) A large nest population inhibits tandem running. Emigrations in which scouts discovered nearly empty nests had significantly more tandem runs than emigrations in which ants discovered nests that had been primed by the experimenter with 15 ants at the start of the emigration. (c) Preventing nest population growth enhances tandem running. Ants that were prevented from leading their tandem followers all the way into the new nest led significantly more tandem runs than control ants whose followers were admitted to the nest (see Pratt *et al.* (2002) for more details.)

already consider the new nest to be their current/real home.

In these ants, both the opinion polling based on threshold numbers of nest-mates at the new nest and also direct comparisons, by some individuals, of different nest-sites may effectively substitute for the absence of a recruitment signal that can directly encode site quality. Direct comparisons might provide an obvious failsafe mechanism to minimize the risk that an inferior nest-site is chosen or

a better site is overlooked due to erroneous information. Examination of the role of direct comparisons began when Mallon *et al.* (2001) gave colonies a binary choice between a good and a mediocre new nest-site. A mediocre nest-site is one that is preferred to a still worse one and will elicit strong recruitment if nothing better is available. In three emigrations by three different colonies that were each given binary choices between good and mediocre nest-sites a grand total of 122 ants exhibited recruitment behaviour (i.e. either tandem running or carrying, or both). One hundred and sixteen recruited to the better site and only a tiny minority recruited either to the poorer site or to both sites. However, 66 of these 122 recruiters visited both sites at some point. Evidence for direct comparison stems from the observation that among these 66 ants, 38 visited both sites before beginning to recruit to either of them and 35 of these 38 initiated recruitment only to the superior site. The three remaining exceptions led tandem runs to the mediocre site before switching their recruitment to the superior one. In these three different experimental colonies 84%, 43% and 32% of eventual recruiters visited both nests, respectively. Thus, there is great variation in the frequency of direct comparison and two colonies chose the better nest after relatively little direct comparison. In all cases, however, there is much more direct comparison than the 5% or so observed among honeybee house-hunting scouts (Camazine *et al.* 1999).

In the next section, we will compare and contrast mathematical models for these decision-making processes in honeybees and *L. albipennis*.

5. MATHEMATICAL MODELS FOR INFORMATION FLOW AND ADAPTIVE HOUSE-HUNTING DECISIONS

Mathematical models of nest-site choice in honeybees and ants serve to highlight the underlying logic and dynamics of these decision-making systems. They also help to show which processes are well understood and which need further experimental investigation. Finally, they are a useful starting point from which to begin the process of drawing generic insights from these studies of information exchange and adaptive decision-making.

To build a model, we consider the series of behaviours which individual insects exhibit and the rates at which they change between these behaviours. For the honeybees, Britton *et al.* (2002) have derived a useful model from classical models of the dynamics of disease or rumours in human societies (Kermack & McKendrick 1927; Karmeshu & Pathria 1980). In this model, honeybee scouts proceed through the sequence of behaviours shown in figure 6a. Scouts are at first neutral/naive (the number of bees in this state is X), then on finding and assessing a site i , they begin recruiting (Y_i). Recruiters eventually cease dancing, but remain informed about the site they were advertising (Z_i). In this informed but non-recruiting state, the bees can be recruited by dances either to another site j , or they may be influenced to start dancing for site i again (Visser & Camazine 1999a,b)—however, this is rare unless site i is the best site.

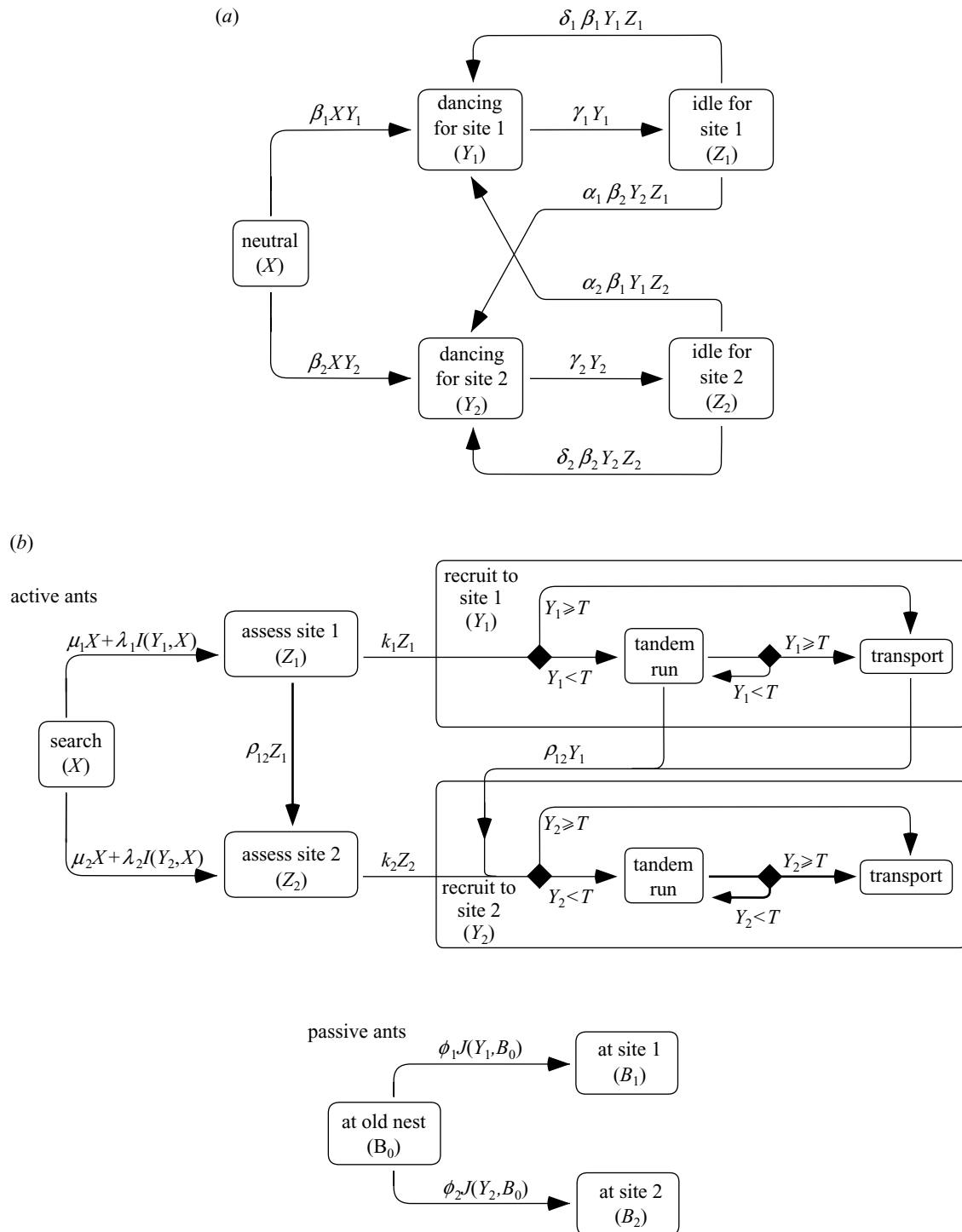
Pratt *et al.* (2002) have modelled the house-hunting behaviour of *L. albipennis* ants. The sequence of behav-

iours by *L. albipennis* is shown in figure 6b. Instead of recruiting immediately after assessing a potential site, the ants spend a variable period of time walking in or near the site or between that site and the old nest. The duration of this period is graded according to site quality, such that worse sites produce longer delays until recruitment begins (Mallon *et al.* 2001). Thus, scout ants go from being naive searchers (X) to being informed of a particular site i but not recruiting (Z_i), to recruiting to the site (Y_i). The recruitment state (Y_i) is broken down further into categories of tandem running and transporting. The switch between these two sub-states occurs when $Y_i = T$, the nest population threshold. Above this threshold, tandem running ceases and ants begin transporting. Once committed to recruitment, ants will not go back to the informed but non-recruiting state. An ant will cease recruitment to a site i only if she comes across a superior potential nest-site. In this case, she will switch her allegiance to the better site (Mallon *et al.* 2001). This switching can be an important part of the colony's decision-making process, because, unlike the honeybees, *L. albipennis* recruiters have a significant chance of independently finding another site.

Although the ordering is different (cf. figure 6a,b), both the ants and the bees have three stages of individual behaviour: scouting, recruiting and being informed without recruiting. This three-stage procedure serves an important role in nest choice. Recruitment by successful scouts allows the colony to quickly learn of a prospective site, whereas the periods of abstention from recruitment ensure that a decision is not reached before other options have been considered. For the ants this abstention occurs during a long initial assessment period, whereas for the bees it takes the form of a 'cooling off' period (but in the bees too, slow (weak) recruitment to poorer sites also provides an opportunity for a swarm to find something better). The abstention periods, or lags, allow other scouts from the old nest to find and report competing sites. In the ants, at least, these lags also give discoverers of one site a chance to find and compare still other sites. One substantial difference between the ants and the bees is that an ant will only stop recruiting to a nest-site if she finds a better one, while the bees cease dancing spontaneously.

Figure 6a,b shows not only the order in which the ants and bees exhibit various behaviours, but also the rate of change of behaviours. These rates are determined, in part, by the nature of the recruitment mechanism. The bees use the waggle dance, a group recruitment signal that can potentially summon several bees to the advertised site. Therefore, the rate at which uninformed bees are recruited to a potential site is $\beta_i Y_i X$, where β_i determines the strength of persuasion through dancing. The parameter β_i encodes the quality of the potential nest-site i ; bees perform more dances for better quality sites. Dancers for site i retire from dancing at rate γ_i . Retirees may resume dancing for the same site i with relative probability δ_i (compared with the rate at which neutral bees start dancing), or they may start dancing for another site with relative probability α_j (also compared with neutral bees).

If sites 1 and 2 are found by the bees simultaneously, then the site that induces the least (vigorous) dancing and fastest retirement (i.e. the site with the smaller value for β_i) will eventually have no bees dancing for it. Henceforth,

Figure 6. (*Caption opposite.*)

for simplicity, we shall assume that $\gamma_1 = \gamma_2 = \gamma$, $\delta_1 = \delta_2 = \delta$, and $\alpha_1 = \alpha_2 = \alpha$. Figure 7a shows a simulation of the model for the bees when site 2 is superior to site 1 but news of site 2 arrives later. In this simulation $\alpha_i = \delta_i$ and the colony consensus always switches to site 2, however late the news arrives. Figure 7b shows a similar situation, except that here α_i is greater than δ_i , implying that bees disdain dancers for the site they already know about in favour of dancers for the alternative site. As a result stalemate persists and no decision is made. In fact, Visscher & Camazine's (1999a) data (for two identical alternative sites) suggest that $\alpha_i = \delta_i$. This may be inferred

from their observation that previously dancing bees follow the dances of other bees seemingly at random.

The tandem running and transports performed by ants are individual recruitment behaviours: recruiters bring one ant at a time to the new nest-site. As a result the recruitment rate of ants to a new site does not depend on the number of potential recruits in the old nest. For the ants, independent discoveries of a particular nest-site (represented by the term $\mu_i X$) can be as important as recruitment. Also, unlike the bees, the parameter governing recruitment rate (λ_i) does not encode quality. Ants do not recruit faster to better sites: once committed to a

Figure 6. (a) Flow chart for the possible dynamics of recruitment in honeybees. The figure shows the order and rates at which the bees switch between behaviours. The following set of differential equations specify the model and determine the structure of the figure.

$$dX/dt = -\beta_1 XY_1 - \beta_2 XY_2,$$

$$dY_1/dt = \beta_1 XY_1 - \gamma_1 Y_1 + \delta_1 \beta_1 Y_1 Z_1 + \alpha_2 \beta_1 Y_1 Z_2,$$

$$dY_2/dt = \beta_2 XY_2 - \gamma_2 Y_2 + \delta_2 \beta_2 Y_2 Z_2 + \alpha_1 \beta_2 Y_2 Z_1,$$

$$dZ_1/dt = \gamma_1 Y_1 - \delta_1 \beta_1 Y_1 Z_1 - \alpha_1 \beta_2 Y_2 Z_1,$$

$$dZ_2/dt = \gamma_2 Y_2 - \delta_2 \beta_2 Y_2 Z_2 - \alpha_2 \beta_1 Y_1 Z_2.$$

The type of decision made is determined by the equilibrium distribution of X , Y_1 , Z_1 , Y_2 and Z_2 (see text and Britton *et al.* (2002) for more details). (b) Flow chart for the possible dynamics of recruitment for the ants. The figure shows the order and rates at which the ants switch between behaviours. The following set of differential equations specifies the model and determines the structure of the figure. Note: the following includes the functions I and \mathcal{J} that show the threshold effect for active and passive ants, respectively. (See text and Pratt *et al.* (2002) for further details.)

$$dX/dt = -(\mu_1 + \mu_2)X - \lambda_1 I(Y_1, X) - \lambda_2 I(Y_2, X),$$

$$dZ_1/dt = \mu_1 X + \lambda_1 I(Y_1, X) - \rho_{12} Z_1 - k_1 Z_1,$$

$$dZ_2/dt = \mu_2 X + \lambda_2 I(Y_2, X) + \rho_{12} Z_1 - k_2 Z_2,$$

$$I(Y_1, X) = Y_1, \text{ if } Y_1 < T \text{ and } X > 0; 0, \text{ otherwise}$$

$$I(Y_2, X) = Y_2, \text{ if } Y_2 < T \text{ and } X > 0; 0, \text{ otherwise}$$

$$dY_1/dt = k_1 Z_1 - \rho_{12} Y_1,$$

$$dY_2/dt = k_2 Z_2 + \rho_{12} Y_1,$$

$$dB_1/dt = \phi_1 \mathcal{J}(Y_1, B_0),$$

$$dB_2/dt = \phi_2 \mathcal{J}(Y_2, B_0),$$

$$\mathcal{J}(Y_1, B_0) = 0, \text{ if } Y_1 < T \text{ or } B_0 = 0; Y_1, \text{ otherwise}$$

$$\mathcal{J}(Y_2, B_0) = 0, \text{ if } Y_2 < T \text{ or } B_0 = 0; Y_2, \text{ otherwise.}$$

The equations above assume that an ant that has begun transporting will revert to tandem running if the population at her site again falls below the quorum. It is not known whether real ants show such reversions, and they never occurred in the model runs presented in this paper. Hence, for clarity, we have omitted reversions from the flow chart.

particular site, an ant will attempt to recruit to that site with the same vigour as she would to any other suitable site. However, the mean delay $1/k_i$ before starting recruitment strongly depends on the quality of the nest i : the better the quality the smaller this is (Mallon *et al.* 2001). The greater delay at inferior nests allows better nests to receive a greater number of ants. One reason for this is that, during the delay, ants may find a better nest, at rate ρ_{ij} per ant per minute. More importantly, the population of ants at a better site will build faster because each ant delays less before starting to recruit. Thus, while the rate of recruitment itself does not depend upon nest quality, the delay in the start of recruitment strongly affects the final choice of nest-site. Figure 8 shows a numerical simulation of the ant model for particular parameter values.

For bees, the emigration of the entire swarm does not usually begin until the vast majority of scouts are dancing for the same nest-site. Similarly, the ants switch from

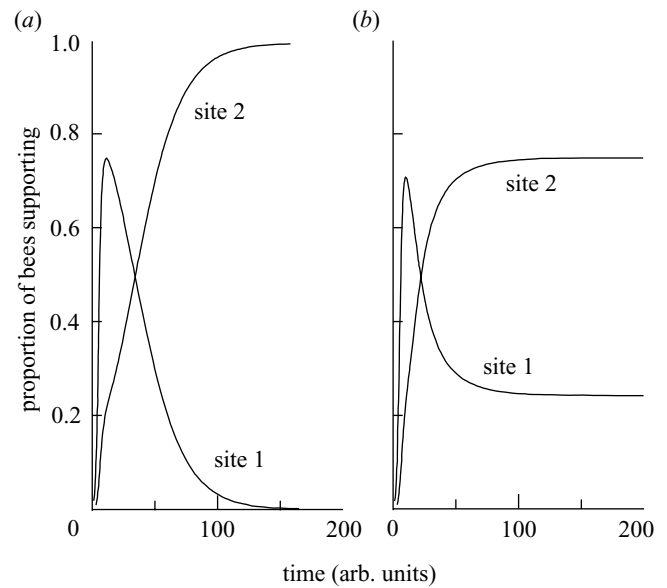


Figure 7. Results from the model for the dynamics of honeybee house-choice dynamics (as in figure 6a). In both panels, $\beta_1 = 1.0$, $\beta_2 = 1.2$, $\gamma = 0.3$, $\delta = 0.5$, so that the second site is marginally superior to the first. For simplicity, we have assumed that $\alpha_1 = \alpha_2 = \alpha$, $\delta_1 = \delta_2 = \delta$ and $\gamma_1 = \gamma_2 = \gamma$. In (a) $\alpha = \delta = 0.5$, the colony consensus always switches to site 2, however late the news arrives. In (b) $\alpha = 0.7$ and no consensus is reached (see Britton *et al.* (2002) for further details).

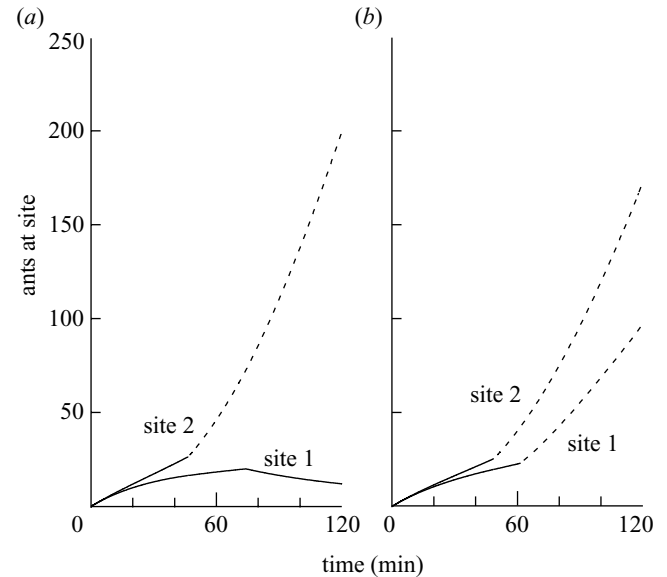


Figure 8. Results from the model for the dynamics of the ant's emigration, determined by the model in figure 6b. In both (a) and (b), site 2 is of superior quality to site 1, but in (b) the difference in quality is smaller. The solid lines indicate the number of ants at the site before transporting begins, while dashed lines indicate that transporting has begun. For (a) no splitting occurs, but for (b) ants are transported to both sites. For both (a) and (b) parameters $\mu_1 = \mu_2 = 0.013$, $\lambda_1 = \lambda_2 = 0.033$, $\phi_1 = \phi_2 = 0.099$ and $T = 10$. The quality of nest 1 differs for the two emigrations, for (a) $k_1 = 0.016$, $k_2 = 0.020$ and $\alpha_{12} = 0.008$ and for (b) $k_1 = 0.019$, $k_2 = 0.020$ and $\alpha_{12} = 0.004$. See Pratt *et al.* (2002) for more details of the model.

tandem running, a relatively slow recruitment process, to directly carrying ants and brood only when a threshold level of ants is found at the new nest. The bees reach consensus over the best new nest-site through the positive feedback of waggle-dance recruitment, combined with the progressive retirement of dancers, with little input from direct comparison of sites by individual bees (Visscher & Camazine, 1999a,b; Seeley & Buhrman 1999). Positive feedback also plays a part in the emigration of *L. albipennis*, but direct comparison of sites can also be important.

Neither the bees nor the ants are always likely to choose the best quality site (figures 7 and 8). If the best site is found too late, or if it is located too far away, then the emigration may end with an inferior site being chosen. However, for any emigration process there is a cost associated with taking too long to decide. The swarm clinging to a tree or the ants left in a destroyed nest are more exposed than when safely moved to a new site. The ants, unlike the bees, will sometimes temporarily split between two nest-sites (see figure 8b). Such splits may not be too costly for *L. albipennis*, given that they often naturally split their nests, at certain times of the year, between two or more sites (Partridge *et al.* 1997). Certainly such splitting is probably preferable to the exposure that would be endured at the old nest. In any event, the ability of ants to compare nest qualities should eventually allow them to reunite in the best nest.

Of great importance to all emigrating societies is that the details of their emigration process are tuned to provide an optimal trade-off between a thorough survey of the quality of available sites and the speed of emigration. Our investigations suggest that natural selection has tuned the parameters of both of these forms of emigration to favour decisions that are both accurate and consensus-based. Obvious examples of tuning are quality-dependent recruitment delays in the ants, and dance vigour and duration in the bees. Some of the parameter tuning is subtler. For example, we found that when $\alpha_i = \delta_i$ the bees were ensured a consensus decision. Biologically, $\alpha_i = \delta_i$ corresponds to informed but non-recruiting bees sampling dances at random. This is counter-intuitive, since rather than preferring dances for new sites, thus increasing the information on which to base a decision, bees just as readily monitor dances for the site they have already visited. Our mathematical model elucidated the reasons for this particular parameter tuning.

The details of *L. albipennis* behaviour are similarly tuned so as to provide a consensus decision. The threshold population at which ants switch from slow tandem running to fast direct transport is high enough to minimize splitting but low enough to ensure a rapid move. Pratt *et al.* (2002) showed that there is a wide range of values for this threshold, which minimizes both the emigration time and the probability of splitting between two sites. In reality, the threshold, for the switch varied among individual ants but lay in the range predicted by the model (figure 5a). The threshold is thus set at a level that prevents too-frequent splitting.

Our mathematical models are rather different to those employed when trying to quantify an optimal behavioural strategy. Although we know that a trade-off between speed and accuracy must be achieved in house hunting, we can-

not accurately quantify the respective pressures to make either a quick or an accurate decision. For example, we do not know the risk incurred by swarming bees when exposed, or the cost to the ants of temporarily splitting between two nests. Rather, the main purpose of our models is to provide a qualitative understanding of the two emigration processes, showing where similarities and differences lie. Our models also show that the emigrations are robust to changes in parameters such as the threshold for switching from tandem running to transport. The mathematics enables us to understand how processes of cooperation and information flow in insect societies are organized, and from this position we can then understand why such processes have been chosen by natural selection.

6. CONCLUSIONS

One of the fundamental issues in decision-making is how much information should one gather before making a decision (Houston *et al.* 1982). For example, Stickland *et al.* (1992, 1993, 1995; see also Britton *et al.* 1998) have shown, through theoretical examination of ant foraging algorithms, that there can be a distinct trade-off between the speed of decision-making and the thoroughness of the survey. Stickland *et al.* (1992, 1993, 1995; see also Britton *et al.* 1998) modelled ants investigating binary trees that culminated in 128 endpoints only a few of which had food rewards. Model ants with recruitment that was too strong, (i.e. positive feedback that was too rapid) swiftly locked all of their foraging onto the first resources they discovered and this prevented a much more thorough search for potentially more rewarding alternatives. However, too-weak recruitment might mean that too few ants would ever focus their foraging efforts on valuable sources. In this case, the colony would continue to put its efforts into surveys and would not fully exploit even a very rewarding site.

An appropriate balance between a lengthy and thorough survey and a relatively rapid decision seems particularly difficult for house-hunting social insects to achieve. The house hunters need to reach a consensus and this would seem to necessitate very strong positive feedback provided by intense recruitment—but just such positive feedback could cause an inappropriate snap-decision that was too rapid to be well informed. The above analysis of the natural history of decision-making by house-hunting honeybees and ants, and its description and interrogation by mathematical modelling, shows how in both cases a compromise is achieved between accuracy and speed. In both cases, lags are built into the dynamics of their deliberations that provide sufficient time for an array of potential nest-sites to be discovered, evaluated and ranked, so that the best may be chosen.

Intriguingly, von Frisch (1954), Lindauer (1961) and Seeley (1985) all suggested that direct comparisons of alternative nest-sites were the key to the decision-making of house-hunting honeybees. For example, Lindauer (1961) stated that 'If those scouting bees which at first had only inferior or average dwellings to announce are persuaded by the livelier dances of their colleagues to inspect the other nesting place, then nothing more stands in the way of an agreement. They can now make a comparison between their own and the new nesting place, and

they will solicit in the cluster for the better of the two.' Seeley (1985, p. 74) stated 'The heart of the decision-making process is the ability of scout bees to switch their preferences among nest-sites. Thus although one scout may discover a particular site, and initially advertise it because it is the best site she knows, if a second scout finds a better site, the first scout will eventually shift her allegiance to the superior alternative. Such switching results from each scout coding the quality of her site in the vigour of her recruitment dances. Exceptional sites are represented by lively dances that last for half an hour or more, whereas mediocre sites merit only sluggish, seemingly unenthusiastic dances. When a scout that has been performing leaden dances encounters one dancing energetically, she reads this scout's dances and flies off to inspect the corresponding site. If her inspection reveals that it is indeed superior, she begins advertising it in her own dances on the swarm... Thus one by one the scouts gradually transfer their attention from deficient sites to ever better ones, and so ultimately reach a consensus about which dwelling place is best.'

However, it is now clear from the recent work of Seeley & Buhrman (1999) and Visscher & Camazine (1999a) that very little direct comparison of nest-sites occurs in house-hunting honeybees and even comparison of dances by scout bees that have already danced for other sites may be far less important than bees ceasing dancing altogether. Less valuable nest-sites are discarded from further consideration more quickly, because the poorer the site the sooner a bee ceases dancing for it: fewer scouts will be directed towards worse sites and more will be directed to better sites that will have been advertised more vigorously. Indeed, the process of all scouts ceasing dancing after a while will cause nest-sites, in effect, to be ranked with the worst ones being discarded most quickly from further consideration.

In *L. albipennis*, sites of lower quality tend to be discarded in favour of sites of higher quality because such qualities feed forwards into recruitment latency times (good sites initiate recruitment sooner rather than later), good sites can be detected by direct comparison, and good sites more quickly achieve the critical head-count threshold that triggers the much faster form of recruitment.

Leptothorax albipennis and honeybee scouts do all of the initial finding and assessment of nest-sites as solitary individuals. Thus, given their comparable abilities to weight many variables it seems that the cognitive tasks faced and solved by these ant and honeybee workers are of roughly equal complexity. Counter-intuitively, however, *L. albipennis* seem to employ at least some direct comparison of different nest-sites by individuals, whereas direct comparison seems to be much less important for the honeybees. One half of all the *L. albipennis* scouts (i.e. 66 out of 122) responded to their own direct comparison of nest-sites by recruiting to the better one (Mallon *et al.* 2001), whereas only between 5 and 10% of honeybee scouts visited the two nest-sites presented to them (Camazine *et al.* 1999). However, this percentage might be higher when both sites are not excellent, as they were in the Camazine *et al.* (1999) study (T. D. Seeley, personal communication). In addition, these ants appear to use some measure of the numbers of their nest-mates present in a new potential nest-site as a trigger to switch from slow

tandem-running recruitment to faster carrying recruitment (Pratt *et al.* 2002). Thus, overall, the small, tiny-brained ants seem to have taken on board one or more additional and very challenging cognitive tasks. First, they directly compare, and possibly even weight, the attributes of different nest-sites (though bees may do this too). Second, they make use of a head count as a surrogate opinion poll. (It is possible that honeybee scouts, late in the decision-making process, also make a head count of other scouts at nest-sites before encouraging the swarm to take off.) The use of a threshold of *ca.* 10–20 nest-mates in a new nest does represent an opinion poll because each scout only recruits perhaps three others by tandem running (Pratt *et al.* 2002). Thus, for more than 10 nest-mates to be present in a new nest, many scouts must have decided that this nest is suitable.

Thus, the present evidence suggests that it is the ants rather than the bees that make most use of direct comparisons. Nevertheless, compared with the elegant dancing of scout honeybees, which usually results in the explosive flight of a single cohesive swarm, the decision-making of *L. albipennis* colonies may seem ponderous, pedantic and pedestrian. The poor, plodding ants seem to combine an inelegant one-by-one recruitment system and an apparently messy merging of their decision-making process into the start of their emigration, which may begin even though part of the colony is still being recruited to an inferior nest-site. Such a comparison to the detriment of the ants would, of course, be belittling. For example, despite the wonderful information content of honeybee dances, the number of bees that follow and successfully find the target of a particular dance is surprisingly low. Estimates of such target finding are only known, as yet, for foraging not for nest hunting, but they are likely to be comparable. One estimate suggests only one successful recruit per two bouts of dancing, each of which involved many dance circuits (Gould *et al.* 1970). A similar value can be indirectly calculated from Seeley & Towne (1992), where, on average, one recruit arrived at the feeder for every 80 dance-circuits, and the median dance length was only six circuits. This suggests that the waggle dance is not a very efficient means of communication, viewed at the level of a single dancer. The apparently sluggish tandem running of *Leptothorax* ants may be much more efficient. However, one of the great benefits of the waggle dance comes into play when large numbers of bees are induced to dance via the positive feedback of successful recruitment. Perhaps the important difference from tandem running is not efficiency, but the concentration of all the dancers into a small place (the dance floor) in which they can be sampled randomly, that is without prejudice, by followers. Indeed, the dance floor is analogous to a bulletin board (T. D. Seeley, personal communication). This allows the population of dancers to provide at a single site integrated signals of relative target quality, something that is not really possible with tandem running. Furthermore, the honeybees may take days to come to a conclusion. For example, among Lindauer's (1955) 19 swarms, 13 moved within 2 days, three moved within 4 days, and one failed to move at all (for two there were no data). The ants, in contrast, may take only 2–5 h fully to select and wholly to inhabit the best available nest, even if they do partly recruit to an inferior nest. Moreover, in the honeybees, Lindauer

(1957) reported certain rare cases in which there seemed to be an aerial tug-of-war between alternative new nest-sites after the swarm had taken off and one swarm that did not move at all from the initial cluster and would not have survived the winter in such an exposed site. Thus, in both the ants and the honeybees occasionally consensus is not achieved.

What are the ultimate reasons for the differences in the decision-making systems employed by honeybees and *L. albipennis* ants during house hunting? In part, the tactical differences may be by-products of selection to solve different foraging problems. Honeybees use their waggle dances to recruit large numbers of nest-mates to large patches of flowers, which may be blooming today and gone tomorrow. *Leptothorax* forage alone, probably seeking tiny soil invertebrates, they do not recruit during foraging but use individual-specific trail pheromones to find their way home (Maschwitz *et al.* 1986). So the honeybees now use their waggle dance during house hunting and the ants use their individual specific trail pheromones both to determine the floor area of potential nest-sites and to trace their route from the old to the new home. There are, however, also strategic differences. The ants are thorough but they can also be exceptionally speedy in their initiation of an emigration. Natural selection may have favoured such speed because of the vulnerability of the ants in the old nest-site and because suitable sites may be relatively common and a poor decision now, or even a split, may be easily corrected later. For the honeybees, however, good nest-sites are probably extremely rare, colony emigrations are one-off events and the colony will build expensive and immovable combs in any site it selects. So they should make a very careful decision, which is virtually irrevocable. One avenue for future research might be to determine the relative availabilities of good nest-sites in both species and the costs of prolonged searches versus the benefits of choosing ideal homes over mediocre ones.

In summary, it is clear that the honeybees and the ants have both evolved systems that favour careful and exceptionally well-informed selection procedures rather than swift and, potentially, badly informed snap decisions. Moreover, at the level of the deep logic of these selection procedures they are notably similar rather than conspicuously different. In both cases, adaptive procrastination is built into their decision-making so that comprehensive surveys are completed. Furthermore, despite the two-orders-of-magnitude difference both in the size of the societies and the size of their individuals, a remarkably similar number of scouts are involved. This may represent an optimized sample size to provide a reasonably accurate opinion poll. Each colony's decision-making is effectively delegated to a relatively small group of scouts—a supreme court—the members of which may either strategically withdraw and abstain after registering their opinions or continue to influence and convince one another before they engage and commit the rest of the colony to a full emigration.

Nest-site choice in these ants and in the honeybees shows how subtle information processing, combined with appropriate decision rules, allows very large groups of individuals, most of which are very poorly informed, to jointly accomplish impressive cognitive tasks and achieve

a good compromise between quick and well-informed decisions.

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