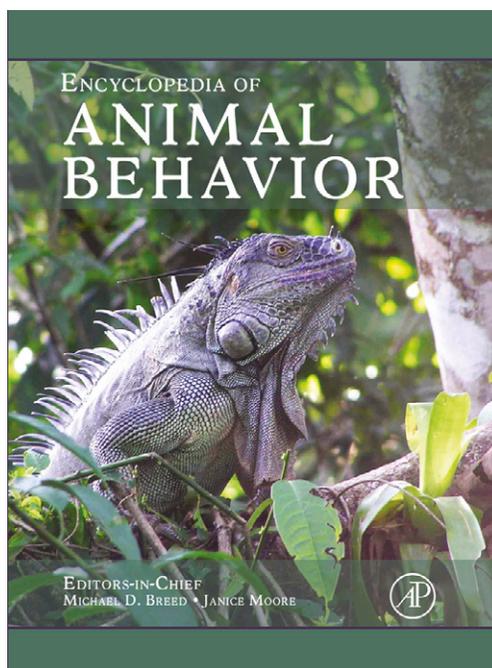


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Nest Site Choice in Social Insects

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Introduction

Social insects are famous for their elaborate nest architecture; less well-known is their skill at moving from one nest site to another. Some, like army ants, move so often that they make no permanent structure, bivouacking instead in simple natural shelters. Others, like honeybees and polybiine wasps, build elaborate nests, but emigrate to new homes during colony reproduction. Still others, like ants of the genus *Temnothorax*, are often forced to move because of the fragility of their nests. House-moving is one of the most challenging tasks a colony faces. Its future success depends on finding a home that offers the right physical environment, protection from enemies, and access to resources. At the same time, choosiness must be balanced with speed, to minimize exposure to a hostile environment, and to prevent delays in growth and reproduction. In most cases, consensus must be reached among hundreds or thousands of individuals, lest the colony should divide among multiple sites to the detriment of all. Finally, all of this must be achieved without well-informed leaders or central control. Instead, the work of selecting and moving to a home is distributed across a population of workers, each informed about only a limited number of options, and influencing only a portion of its nestmates. Social insects have evolved impressively sophisticated solutions to these challenges, making nest site selection a leading model system of the collective intelligence of animal groups. This article reviews what has been learned about the two best-studied groups: *Temnothorax* ants and the honeybee *Apis mellifera*.

Nest Site Choice by *Temnothorax* Ants

Temnothorax are adept house-movers, an ability that is likely related to the fragility of their nests. The best-studied species, *T. albipennis* and *T. curvispinosus*, typically live in rock crevices or hollow nuts. In the laboratory, where most studies have been carried out, they thrive in artificial cavities made from a perforated slat sandwiched between glass slides. Emigrations can be induced by removing the roof slide and providing an intact nest nearby. Over the next few hours, the colony safely relocates to its new home. This process is best understood by considering the simple case when only one site is available, before turning to the more complex problem of deciding between sites.

Organization of Colony Migration

Emigrations are organized by a minority of active scouts, roughly one-third of the colony's workers. Each of these scouts sets out from the damaged nest to find a new home, thoroughly inspecting any candidate that she finds. If it passes muster, she returns to the old nest to inform other scouts of its location. She uses a behavior called tandem running, in which she attracts a single recruit to follow her toward the new site (Figure 1(a)). Their progress is slow and halting, as the leader must pause frequently to allow her follower to catch up. The pair often lose contact for good before reaching the site, but even these broken tandems recruit ants, because the orphaned follower enjoys a higher chance than a naive searcher of finding the target.

Tandem followers make their own assessment of the site and may also begin to recruit. The resulting positive feedback increases the site's population until it reaches a critical level and triggers a dramatic change in behavior. Scouts cease tandem runs from the old nest, and instead begin to carry nestmates, one at a time, to the new site (Figure 1(b)). These transports are roughly three times faster than tandem runs, and population growth accelerates sharply. Over the next few hours, the entire colony is brought to its new home.

Emigration is thus divided into two phases. In the first, discoverers use tandem runs to bring fellow scouts to their find. In the second, the assembled corps of scouts transports the bulk of the colony. Transported ants are generally not scouts, but members of the colony's passive majority, including brood items and queens. This change in targets may explain the difference in recruitment methods. Speedy transports are better for efficient movement of a large number of nestmates, but a scout needs more than quick transit. She must also learn visual landmarks that mark the route, so that she can later navigate independently. A tandem follower is better positioned to learn than a transported ant, because she adopts the same posture she will later use when recruiting on her own.

How does a scout decide when to switch from the first phase to the second? After completing a tandem run, she assesses the population at the new site, apparently through her rate of physical encounters with other ants. Once this population attains a threshold level, or quorum, she switches to transport (Figure 1(c)). Quorum-sensing is a logical way for scouts to tell when they have assembled enough transporters. It can also save them from

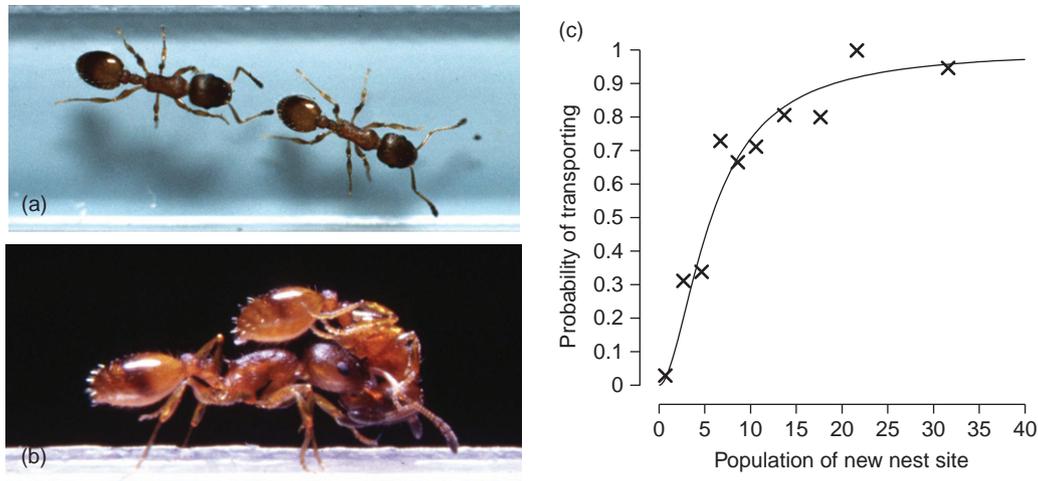


Figure 1 Recruitment behavior used in emigration by *Temnothorax* colonies. (a) Tandem run, in which a single ant is slowly led to a candidate site. (b) Social transport, in which a single nestmate is rapidly carried to the new site. (c) Quorum rule for switching from tandem runs to transports: Crosses show the proportion of ants deciding to transport, rather than lead a tandem run, as a function of the population of the site being recruited to. Line shows a nonlinear function fit to these data.

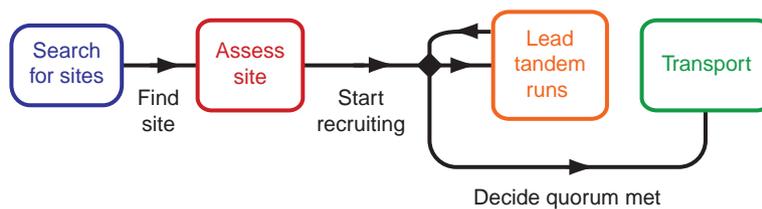


Figure 2 Summary of the decision algorithm used by scout ants during collective nest site choice.

unnecessary recruitment to a site that is near the old nest and easy to find, such that independent discoveries bring an adequate corps of transporters.

There is, however, another dimension to quorum attainment: it marks the last in a series of increasing levels of commitment to a site. A scout enters the first level when she decides to search for a new nest, spurred by the inadequacy of her current home. The second level begins when she finds a candidate and assesses its quality. If she judges it good enough, she advances to the third level in which she recruits fellow scouts to evaluate the site. The final level comes only when quorum attainment indicates that these others have confirmed her judgment by continuing to visit or recruit to the site. From that point on, she pays no further attention to population, and will continue to transport even if the site is experimentally emptied of nestmates.

This series of steps constitutes a decision algorithm that guides scout behavior (Figure 2). The algorithm clarifies two otherwise puzzling observations. First, a scout that has found the new site but not yet sensed a quorum will sometimes retrieve isolated brood items. She carries these not to the safety of the intact new site, but to

the destroyed old nest. Second, after sensing quorum attainment, many scouts lead ‘reverse’ tandem runs from the new nest back to the old. Both behaviors make sense if we assume that recruitment behavior is described by two simple rules: tandem runs are only led away from home to a place where work needs to be done, and transports are made only toward home to repatriate lost or misplaced nestmates. Before a scout senses a quorum at a new site, the old nest is still her home, despite being heavily damaged. She transports lost ants there, and she leads tandem runs away from there to summon help in assessing a candidate site. Her allegiance switches to the new site only when it attains a quorum. From then on, she transports ants only to her new home and she leads tandem runs away from there to summon help in retrieving misplaced ants.

Collective Decision-Making Among Nest Sites

In most cases, colonies confront many candidate homes and must decide among them. Laboratory experiments show that colonies have strong preferences and are adept at choosing a favored site among a group of inferior

competitors. They care about many site attributes, but give particular weight to having an intermediate cavity size and a small entrance. These features likely contribute to nest defense, the accommodation of future growth, and the regulation of internal nest environment. Ants also strongly favor a dark interior, perhaps as an indirect cue of nest wall integrity. Context matters as well, and ants avoid sites that are too close to competing colonies or that contain corpses of conspecific ants. Colonies integrate all of these attributes when assessing sites, weighting them according to importance.

Nest site choice is a challenging task, with inherent tradeoffs between decision speed, accuracy, and unanimity. A colony can improve its chances of finding the best site by evaluating many candidates, but this will take time and make it harder to winnow alternatives to a single choice. Coordination is also challenging, as scores or hundreds of ants must achieve consensus without any single ant learning about all sites, choosing the best and directing others to go there. Instead, the decision is shared by the population of active scout ants, each knowing only a subset of the options. In essence, the decision results from a competition among recruitment efforts at different sites, driven by two key components of the behavioral algorithm described earlier: quality-dependent recruitment initiation and the quorum rule.

Quality-dependent recruitment initiation

When a scout finds a site, she typically does not recruit to it right away, but first makes several visits in between trips to the old nest or further search of the surrounding landscape. The interval until the start of recruitment can be quite long, but it will be longer, on average, for worse than for better sites. That is, each scout conditions her probability of starting to recruit on her assessment of site quality. This effect is amplified by the positive feedback inherent in recruitment, because the scouts brought to a site will themselves initiate recruitment at a quality-dependent rate. This leads to faster population growth at a better than a worse site, driving the colony toward selection of the better site.

From the point of view of an ant that has found a mediocre site, this rule amounts to an investment of time to improve the colony's chances of finding a better option. The balance of exploitation versus exploration is a fundamental problem for any animal engaged in search, whether for a nest site, a mate, or a food source. If options are encountered sequentially, the animal must decide whether to settle for its current discovery or to search for a better one. A scout that delays recruitment to a site is essentially opting for further search. There is an interesting difference between her behavior and that of a solitary animal: her delay in recruiting buys time not only for her own search efforts, but also for those of her nestmates. Thus, she enhances

the colony's search effort, even if she herself never sees another site.

An advantage of this rule is that it allows a colony to hold out for an ideal site, but to settle eventually for the best that can be found. If only a mediocre site is available, ants will recruit to it, although it will take them longer to do so. As a result, colonies offered a choice between a good nest and a mediocre nest will nearly always choose the good one, but the same colonies offered a choice between a mediocre site and a still worse one will nearly always choose the mediocre one.

Quorum rule

The ants' quorum rule amplifies the quality-dependent recruitment effect. Once a site attains a quorum, the switch from slow tandem runs to speedy transports accelerates population growth. On average, a better site will experience this acceleration sooner, allowing it to expand its lead over inferior competitors. The quorum rule favors better nests by imposing an extra level of scrutiny. Each scout relies not only on her direct assessment of a site, but also on an indirect cue about the judgments of other ants. She fully commits only if some minimum number vote with their feet by spending time at the site. This rule can filter out errors by a small number of ants that start recruiting immediately to a site that is not very good.

This description of nest-site choice is somewhat idealized. Colonies may split between sites or even move into an inferior candidate, especially when moving rapidly under duress or when an inferior site happens to be very close to their current home. When this happens, the colony must launch a second emigration from the inferior to a better site. These multistage migrations are suboptimal outcomes, given the likely dangers of exposure during transport and the risk that the colony never reunites. The ants' decision algorithm does not eliminate these dangers, but it minimizes them by reducing the likelihood of splitting between sites.

It is tempting to divide emigrations into an early deliberative phase and a later implementation phase, with the boundary marked by quorum attainment. There is some value in this distinction, but these functions are really not so well separated. Decision-making continues after quorum attainment, most obviously when a temporary split must be resolved by secondary emigrations. At a more basic level, individual ants do not cease to assess a site's quality just because it has attained a quorum. Even those scouts that arrive at a nest after it has grown quite populous still condition their recruitment on its intrinsic quality. Scouts always consider both their own direct assessment of a nest and the 'votes' of their nestmates.

Speed/accuracy tradeoff

A crisis caused by nest destruction is not the only occasion for house-moving. A colony inhabiting an adequate nest

will emigrate if a better site becomes available. In these unforced emigrations, colonies take far longer to finish the move, but their performance is much better, with less splitting between sites. This difference illustrates a fundamental tradeoff between speed and accuracy that is faced by all decision-makers. *Temnothorax* colonies have the ability to shift their stress from one to the other, sacrificing accuracy for speed when pressed to end their dangerous exposure, but investing time for a better result when urgency is less.

Interestingly, colonies use the same behavioral algorithm regardless of urgency, but they tune it for each setting. In a crisis, each active ant moves more rapidly through the algorithm's increasing levels of commitment to a site. The most striking change is their higher rate of recruitment initiation to a candidate site, and models suggest that this has a large effect on the speed/accuracy tradeoff. By delaying recruitment longer in less urgent circumstances, ants invest more in search, at the cost of taking longer to complete the move. More search effort improves chances of finding the best site, but the colony also gains in discriminatory power. When latencies are long, so are the differences between those at better versus worse sites. Greater latency differences mean greater differences in population growth, and thus a greater likelihood that a better site outstrips lesser ones to become the colony's choice.

Individual comparison

In the process described earlier, comparison among sites is an emergent property of the whole colony, not an activity of well-informed individuals. This does not mean, however, that individuals lack this capacity. Scouts almost certainly compare candidate sites with their current home, as indicated by their unwillingness to abandon an adequate nest unless they find a significantly better one. Simulations suggest that this ability is needed for a colony to settle stably in a site, rather than constantly initiating new emigrations. Whether a single ant can also pick the better of two candidate sites is less certain. Ants may simply forget about a nest if they leave it without recruiting, or they may retain a memory of it that causes them to ignore any subsequent finds of lower quality. Such comparisons are potentially quite important, given that a quarter or more of active ants are seen to visit multiple sites, at least in small laboratory arenas. Even without direct comparisons, emigrations may be strongly influenced by these ants, because of the opportunities created for better sites to divert potential recruiters from lesser ones.

Individual comparison is also relevant to rational decision-making, which requires that options be consistently ranked according to intrinsic fitness value, and not by comparison to available alternatives. Irrationality is commonly seen when decision-makers are faced with options that vary in multiple attributes, such that none is clearly

superior. Some strategies for resolving these difficult choices involve direct comparisons among options and can lead to irrational outcomes such as intransitivity or preference reversals. Faced with one such context, *Temnothorax curvispinosus* colonies behave quite rationally, possibly as a result of their highly distributed mode of decision-making, in which most ants lack the opportunity to make direct comparisons.

Nest Site Choice by HoneyBees

The house-hunting behavior of honeybees has many similarities to that of *Temnothorax*, but also many revealing differences. Like the ants, honeybees are cavity nesters, at least in the temperate zone, where house-hunting has been best studied. Colonies show strong site preferences based on multiple criteria, including cavity volume, entrance size, and entrance location. Honeybees sometimes abandon a nest site and move to a new one, typically when foraging conditions deteriorate, but house-hunting most often occurs during colony reproduction. A colony's queen, along with about one-third of its workers, bequeath their nest to a new daughter queen and the remaining workers. The departing bees settle as a compact swarm on a tree branch or similar site. From this bivouac, the bees spend up to several days scouring the countryside for candidate sites, deliberating among them and choosing one as their new home.

Collective Decision-Making

Like *Temnothorax*, bees rely on a competition among recruitment efforts at different sites, carried out by a minority of nest site scouts. These scouts, numbering only a few hundred of the swarm's several thousand bees, travel up to several kilometers from the bivouac. Upon finding a candidate home, typically a tree hole or similar cavity, a scout inspects it closely. If its quality is sufficient, she returns to the swarm and uses waggle dance communication to inform other bees of its distance and direction. Her dancing also encodes the quality of the site, principally as the number of dance circuits she completes during her stay at the swarm. The more circuits, the more opportunity for followers to read the dance, and so the more new bees show up at the site. The recruits themselves may join in advertising the site, also tuning their number of dance circuits to site quality. The result is a positive feedback cascade that swells the number of scouts visiting the site, but at a rate that depends on site quality.

The swarm's corps of scouts typically find many possible homes, and dances are present for several candidates at the same time. How does the group settle on a single one? It was once thought that the decision was made on the swarm's dance floor, on the basis of the typical course

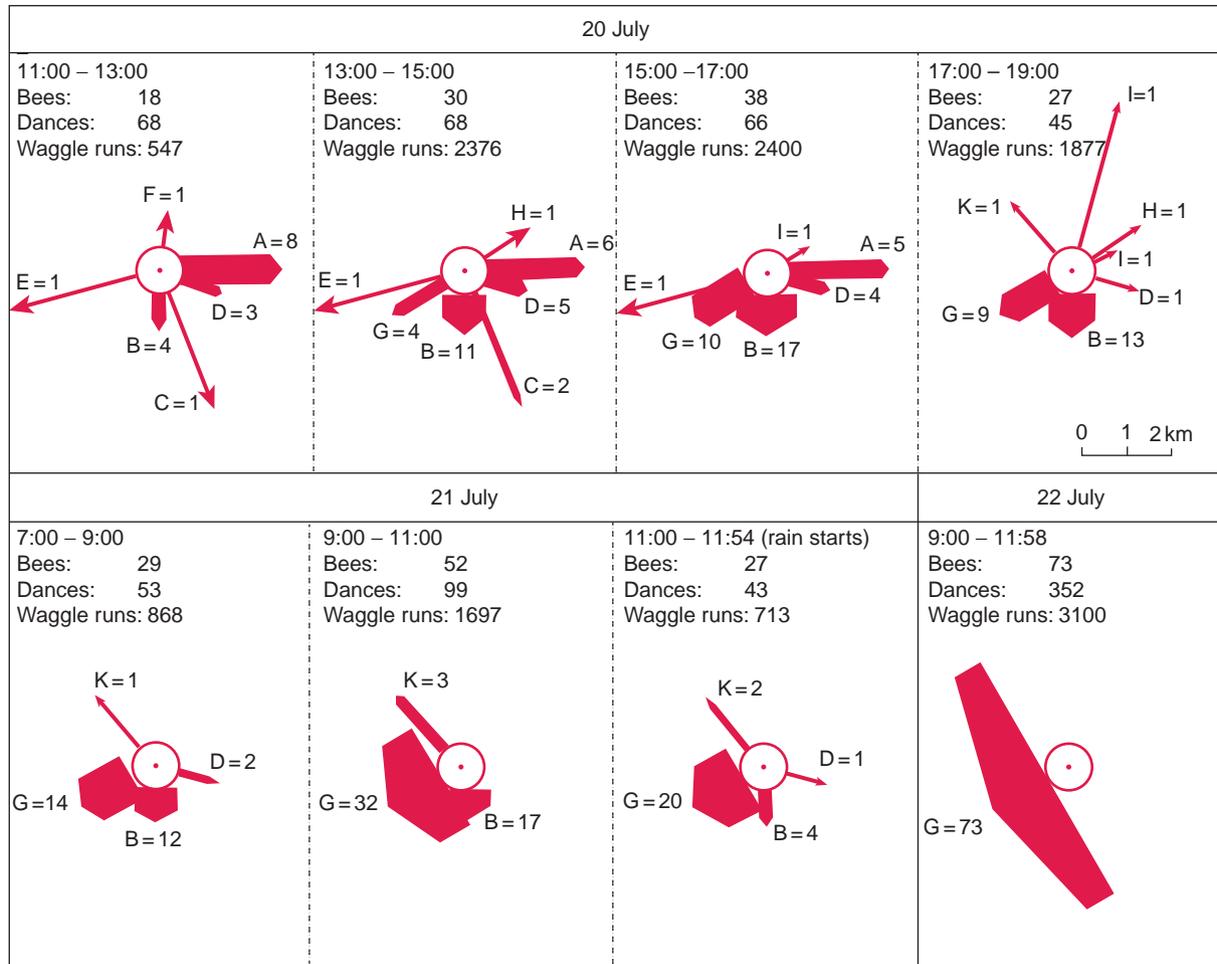


Figure 3 Summary of a honeybee swarm’s decision process over 3 days. Each panel shows the number of dancers, dances, and waggle runs during a 1–3 h interval. The circle represents the swarm, and each arrow represents the distance and direction of a candidate nest site. The thickness of the arrow correlates with the number of bees advertising that site in the interval, also given by the number next to each site’s letter designation. The swarm considered a total of 11 sites, but with no clear leader until the second half of the process, when site G gradually gained support and became the target of all the dances. Adapted from Seeley TD and Buhman SC (1999) Group decision making in swarms of honeybees. *Behavioral Ecology and Sociobiology* 45: 19–31, with permission from Springer.

of events there: the number of advertised sites diminishes over several days until only one remains, and the swarm lifts off and flies to this site (Figure 3). It now appears, however, that a dance consensus is not the trigger that tells the bees that a choice has been made. Instead, like *Temnothorax*, each scout monitors her candidate site to determine when its population has reached a quorum. Upon sensing this, she returns to the swarm and pushes her way through it, delivering a brief vibrational signal called piping to scores or hundreds of bees. Piping stimulates recipients to warm up for flight by shivering their wing muscles. Within an hour, the flight-ready bees are prompted to lift off by buzz-runners, who break up the cluster of bees by burrowing rapidly through it. Interestingly, a similar combination of piping and buzz runs is also

used earlier in emigration, to instigate the swarm’s initial departure from its natal nest.

Once aloft, the diffuse but cohesive group flies directly for the new site. This is an impressive feat of collective orientation in which thousands of bees, 95% of them ignorant of their destination, travel up to several thousand meters to a pinpoint goal. An early hypothesis held that the bees are guided by pheromones released from the Nasonov glands of informed scouts. This does not appear to be the case, since sealing shut the glands of all swarm members does not interfere with normal orientation. Experiments and models better support the ‘streaker bee’ hypothesis, which holds that knowledgeable scouts point the way by flying through the swarm at high velocity in the direction of the target site.

Quorum Sensing, Attrition, and Consensus

As in the ants, quorum sensing amplifies a difference among sites created by quality-dependent recruitment effectiveness. Better sites experience faster population growth and so are more likely to reach a quorum and trigger lift-off. For the bees, however, quorum attainment is a much clearer watershed than it is for the ants. It marks the shift from a deliberative period lasting several days to an implementation period that may take only 1 h. This sharper distinction facilitates consensus on a single site by reducing the time window for a second site to reach a quorum. Indeed, bee swarms do not tolerate splitting between sites. If there is disagreement among scouts when the swarm lifts off, it soon resettles and continues to deliberate. This difference from the ants may be rooted in a greater cost of splitting for bees. Division of the swarm leaves one portion queenless and doomed to early extinction, as the workers cannot lay the fertilized eggs necessary to rear a new queen. *Temnothorax* colonies have brood from which new reproductives can be reared, and some colonies have multiple queens.

The importance of consensus for the bees is also suggested by another distinctive feature of their decision-making: dance attrition. Unlike *Temnothorax* recruiters, each honeybee dancer eventually ceases advertising a site, even before the swarm has reached a decision (Figure 4). This applies even to dancers for an excellent site, although it takes longer for their activity to decline from its high initial levels. An important effect of attrition is to slow population growth at each advertised site. Overly effective dancing poses the danger that more than one site will reach a quorum at the same time. This means either that the colony remains deadlocked or that it splits with disastrous consequences. By moderating recruitment strength, attrition lengthens the intervals between quorum attainment at different sites. It also fosters the achievement of a dance consensus. Although this consensus does not trigger the swarm's decision, it typically coincides with it, and it may help to avoid abortive lift-offs.

Another interesting difference from the ants is the lesser role for comparison or switching among sites by individuals. Given the importance of unanimity to the bees and their reliance on a centralized advertising location, it might be expected that scouts commonly follow one another's dances and determine for themselves which advertised site is best. Although such comparisons may occur, they appear not to be an important component of the swarm's decision. Very few scouts visit more than one site, and experimental suppression of comparison does not hinder the swarm's ability to settle on a single site.

Conclusion

A striking similarity between honeybee and ant emigration is the central role of quorum-sensing in coordinating

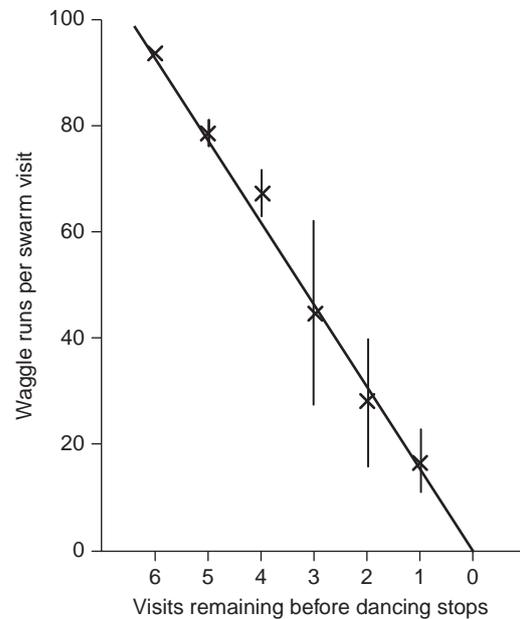


Figure 4 Scouts decrease their number of waggle runs with each successive visit to the swarm, eventually ceasing to dance altogether. This applies regardless of site quality, but bees advertising better sites start with a larger number of dance circuits, and so persist longer at dancing than bees advertising worse sites. Adapted from Seeley TD (2003) Consensus building during nest-site selection in honeybee swarms: The expiration of dissent. *Behavioral Ecology and Sociobiology* 53: 417–424, with permission from Springer.

behavior. The quorum rule provides a solution to a general dilemma faced by social organisms that must reach consensus decisions. On the one hand, they can benefit from the 'wisdom of crowds' if they filter out individual errors by taking into account the independent judgments of many individuals. On the other hand, if individuals are too independent, the group will have difficulty reaching consensus on a single option. The quorum rule offers a compromise between these demands: social influences are weak when exerted by only a few individuals, but their impact grows sharply once the numbers advocating an option surpass a threshold. This strategy is not exclusive to ants and bees. Many social animals, including fish, birds, and arthropods, use analogous threshold rules to optimize the integration of personal and social information.

The tradeoff between speed and accuracy is another general decision-making issue that emerges in both ants and bees. Effective discrimination among options improves with information, but gathering information requires an investment of time. Both ants and bees adopt strategies that markedly slow their decision-making, but make it more accurate. At least for ants, these measures can be adjusted to accelerate emigration at the cost of accuracy in urgent conditions. Individual decision makers face a fundamentally similar tradeoff and also have means

to adaptively tune their behavior according to context. Their choices emerge from a neural network rather than a social one, but both systems address the same challenge and may use similar strategies. Thus, the future study of both individual and collective intelligence may benefit from seeking evidence of common solutions.

See *also*: Collective Intelligence; Communication Networks; Consensus Decisions; Decision-Making: Foraging; Distributed Cognition; Group Movement; Honeybees; Insect Social Learning; Rational Choice Behavior: Definitions and Evidence; Social Information Use.

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