

Sensory coding of nest-site value in honeybee swarms

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SUMMARY

This study investigates the first stage of the decision-making process of a honeybee swarm as it chooses a nest site: how a scout bee codes the value of a potential nest site in the waggle dances she produces to represent this site. We presented honeybee swarms with a two-alternative choice between a high-value site and a medium-value site and recorded the behavior of individually identifiable scout bees as they reported on these two alternatives. We found that bees performed equally lengthy inspections at the two sites, but that, on the swarm cluster, they performed more dance circuits per bee for the high-value site. We also found that there was much individual-level noise in the coding of site value, but that there were clear population-level differences in total dance circuits produced for the two sites. The first bee to find a site had a high probability of reporting the site with a waggle dance, regardless of its value. This discoverer-should-dance phenomenon may help ensure that a swarm gives attention to all discovered sites. There was rapid decay in the dance response; the number of dance circuits produced by a bee after visiting a site decreased linearly over sequential visits, and eventually each bee ceased visiting her site. This decay, or 'leakage', in the accumulation of bees at a site improves a swarm's decision-making ability by helping a swarm avoid making fast-decision errors.

Key words: sensory coding, group decision making, nest-site selection, *Apis mellifera*.

INTRODUCTION

Over the last two decades, significant progress has been made toward understanding the mechanistic basis of decision making, both in individual animals (Schall, 2001; Glimcher, 2003; Sugrue et al., 2005) and in animal groups (Pratt et al., 2002; Passino et al., 2008). Decision making is an important topic for neuroscience and sociobiology alike because of its pivotal role in translating sensory inputs into the adaptive actions of individuals and groups. The translation process involves building a sensory representation of the external world, then transforming this sensory representation into a decision, and finally implementing the chosen course of action (Fig. 1). The most striking progress toward understanding the neurobiology of individual decision making has been made in studies of eye-movement choice in monkeys (Schall, 2003; Smith and Ratcliff, 2004). The strongest progress toward understanding the sociobiology of group decision making has been made in studies of nest-site choice in colonies of ants and bees (Franks et al., 2002; Seeley et al., 2006; Visscher, 2007).

There is a remarkable consistency in the pictures that have emerged from studies of neuronal activity associated with eye-movement decisions by monkey brains and from studies of individual activity associated with nest-site decisions by honeybee swarms. In both cases, the decision-making process is essentially a race between competing accumulations of evidence in support of the various alternatives, with the choice determined by which accumulation first reaches the threshold level of evidence needed for a response. In monkey brains, the build-up of information underlying the choice of an eye movement to the left, for example, takes the form of increased firing by neurons in oculomotor areas that respond selectively to leftward motions (Newsome et al., 1989; Glimcher, 2003). Similarly, in honeybee swarms, the build-up of information underlying the choice of a nest site to the north, for example, takes the form of increased numbers of scout bees visiting

the northern site (Seeley and Visscher, 2004). Furthermore, both in monkey brains and bee swarms, the decision-making system includes mutually inhibitory linkages between the different sites of evidence accumulation, a feature that boosts the likelihood that only a single alternative is chosen, the one with the highest evidence total (Shadlen et al., 1996; Passino et al., 2008).

Another feature of the decision-making process that monkey brains and bee swarms have in common is sequential sampling of sensory information. That is, they do not base their decisions on a single, instantaneous sampling of sensory information, as is typically assumed in signal-detection theory (Green and Swets, 1966), but instead they gather sensory information over periods lasting up to several seconds (monkey brains) or several hours (bee swarms). If the sensory information is noisy, then acquiring it over time in multiple samples will minimize the effects of noise in the sensory system and thereby improve the reliability of the decision making. Prior studies of the sensory-transformation component (Fig. 1) of decision making by honeybee swarms have shown how a swarm's sensory units (scout bees) produce signals (waggle dances) on the surface of the swarm that form a sensory representation of the alternative sites, and how this sensory representation stabilizes over the course of a decision-making event (Lindauer, 1955; Seeley and Buhrman, 1999; Passino et al., 2008). Previous studies have also shown how the signals produced by a swarm's sensory units show a pattern of rapid response decay, i.e. decreased response over time to a constant stimulus (potential nest site) (Seeley, 2003; Visscher, 2003).

One important aspect of the sensory-transformation component of a swarm's decision-making process that remains poorly studied, however, is exactly how the bees code the value of a potential nest site in the waggle dances produced to represent this site. The sensory coding of nest-site value is critical to the decision-making process, for it is what gives better sites an advantage over poorer sites in the

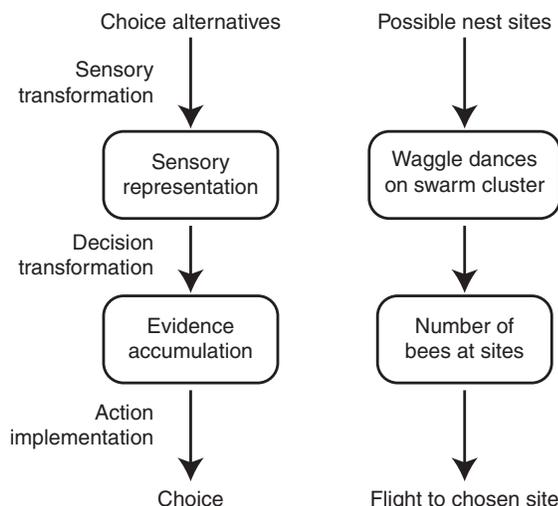


Fig. 1. Conceptual framework for decision making that illustrates the processing stages for making a decision (left) and the application of this framework to the mechanisms of nest-site choice by a honeybee swarm (right). A sensory transformation takes primary sensory input and generates an internal representation of the alternatives, including a coding of their values. A decision transformation uses this sensory representation to build a distribution of evidence among the alternatives, with more evidence accumulating at the higher value alternatives. A final processing stage produces the actual decision, transforming the evidence distribution into a discrete choice of action. Adapted from Sugrue et al. (Sugrue et al., 2005).

competition among sites to accumulate the threshold number of affiliated scout bees. Lindauer (Lindauer, 1955) stated that scouts reporting better sites perform longer and livelier dances, but his evidence was limited. To give us solid information on this topic, we presented honeybee swarms (one at a time) with a two-alternative choice between a high-value nest box and a medium-value nest box, and we recorded the behaviors of the scout bees as they reported on these two alternatives. Specifically, we recorded the strength of each waggle-dance signal produced by individually identified scout bees as they provided the swarm with sensory information on the two nest boxes. These recordings reveal not only how the signals for the high- and medium-value alternatives differed in average signal strength, but also how much signal noise there can be in a swarm's sensory information about alternative nest sites.

MATERIALS AND METHODS

Study site and experimental setup

The experiment was conducted at the Shoals Marine Laboratory on Appledore Island, Maine (42°58' N, 70°37' W). This 39 ha island is nearly treeless and has few buildings; hence it has few natural nest cavities for honeybees. Here, we could set out our nest boxes and be confident that they would receive attention from the scouts bees of our swarms.

The swarms we used were artificial swarms of honeybees (*Apis mellifera* L.) prepared one at a time from four colonies that we brought to the island. Each colony was headed by a 'New World Carniolan' queen purchased from Strachan Apiaries in Yuba City, CA, USA. We prepared a swarm by shaking 1.0 kg of bees, about 8000 individuals, from the combs of a hive into a screen cage with their queen in a smaller cage among them, feeding this cage of bees with sucrose solution (1:1 sucrose:water by volume) for 3 days. The production of abundant wax scales signified that these bees had shifted into a condition like that of a natural swarm, and we then

Table 1. Locations of the nest boxes and number of scout bees monitored at the 401 and 151 nest boxes in each of the seven trials of the experiment

Swarm	Date	Location of nest boxes	Recording period (h)	No. of scouts	
				401	151
1	11 July 07	Broad Cove	15:40–18:25	5	5
	12 July 07	Devil's Glen	10:15–15:10	6	5
2	16 July 07	Devil's Glen	09:22–12:25	7	6
	17 July 07	Broad Cove	09:33–12:00	5	6
3	21 July 07	Broad Cove	09:12–13:30	7	4
	22 July 07	Devil's Glen	12:14–14:45	5	6
4	25 July 07	Broad Cove	15:09–17:30	6	5
			Total	41	37

set them up on a stand for observation. The swarm stand was that described by Seeley and Buhrman (Seeley and Buhrman, 1999). This stand spread the swarm out over one surface of a board, so that activities on the swarm's surface could be more easily monitored.

We set up each swarm, one at a time, on a porch of the old Coast Guard building, and positioned two nest boxes 40–50 m apart, either 240 m to the north of the swarm, near Broad Cove, or 250 m to the east of the swarm, near Devil's Glen [roughly, sites 1 and 5 shown in figure 2 in Seeley and Buhrman (Seeley and Buhrman, 2001)]. The distance of each nest box from the swarm site was determined via GPS using a Garmin GPSMAP 76 receiver (Garmin International, Olathe, Kansas, USA). Table 1 shows for each trial when it was performed, where the nest boxes were located, and how many scout bees were monitored. For most of the swarms, we conducted two trials on two consecutive days, with the two nest boxes moved from the Broad Cove location to the Devil's Glen location (or *vice versa*) at the end of the first trial, so that in the second trial the swarm had to start over in its search for a home site. At the end of each trial, we collected the scout bees that we had monitored during that trial, so different bees were studied in each trial. The two nest boxes used in this study were the same as those used in a previous study on the island (Seeley and Buhrman, 2001). The cavity volume of these nest boxes is adjustable, and in the present study we set one nest box to 401 to provide a high-value nest site, and one to 151 to provide a medium-value nest site. (Colonies in 401 hives have a higher probability of winter survival than those in 151 hives: $P=0.74$ and 0.28 , respectively; Seeley, unpublished data. This is because the former have larger stores of honey, which is the 'heating fuel' of an overwintering honeybee colony.) Each box was housed in a separate, open-fronted shelter [see figure 1 in Seeley and Buhrman (Seeley and Buhrman 2001)] so that the two nest boxes had the same exposure to the wind, sun and rain.

Scout bee marking

After the swarm was set up, an observer was stationed at each nest box, where he/she waited for scout bees to arrive. When a scout arrived, she was caught in a 15 cm diameter, 40 cm deep insect net, either by placing it over the nest box entrance while the bee was inside or by catching her in flight. The bee was then marked with one or two spots of shellac-based paint, while trapped in the net, and then released into the nest box, through its entrance. The paint marks were applied in such a way that the bees were individually identifiable (von Frisch, 1967). This procedure was repeated for the first four to seven scout bees that appeared at each nest box (see Table 1); up to several dozen other scout bees also visited each nest

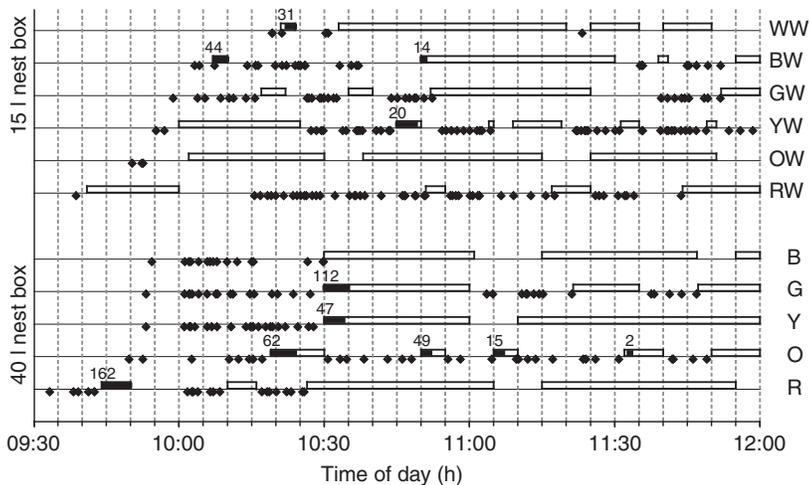


Fig. 2. Activities of the 11 marked scout bees in the 17 July 2007 trial. In the horizontal timeline for each bee, black diamonds denote sightings of the bee at the nest box, white bars show blocks of time at the swarm cluster, and black bars within the white bars indicate periods of waggle dancing. Numbers above the black bars specify the number of dance circuits performed. Color code of bee marking: R, Red; O, Orange; Y, Yellow; G, Green; B, Blue; W, White; RW, Red-White, etc.

box. When not engaged in marking scout bees, the observer at each nest box watched the entrance of the nest box and recorded on a data logger (Tandy Model 102 computer, running a program that maps keystrokes to individual bee identities and creates a text record of the times of such keystrokes) each time he/she observed a particular scout bee at the nest box. These logged data on marked scout sightings gave us precise information on the time that each marked scout spent at the nest box each time she visited it (a scout bee typically makes multiple visits to a potential nest site). Also, every 10 min, the observer counted the number of scouts (marked and unmarked) that were visible outside the nest box.

Swarm observations

Meanwhile, at the swarm cluster, a third observer waited for the marked scout bees to return and perform waggle dances on the cluster's surface. All their dances were recorded on videotape. To build a record of when each marked scout bee was at the swarm cluster, the observer scanned the swarm's surface every 5 min and noted which marked scouts were present; this yielded a record of bee presence/absence for each marked bee for each 5 min block of time. The observer was also able to notice 60% of the marked bees' arrivals at and departures from the swarm, and these records gave us a more detailed picture of when each marked scout was at the swarm cluster.

Data transcription and analysis

We played back the videotapes of each swarm and noted when each marked scout performed a waggle dance and how many circuits of the waggle dance she performed. Each scout bee visited and reported on just one of the two nest boxes during the course of a trial. Because scout bees tend to make repeated visits to potential nesting sites, and can perform a waggle dance after each visit, we determined for each marked scout, (1) her record of signaling (dancing) during each return to the swarm from the nest box, and (2) her total amount of signaling (total number of dance circuits produced to advertise a nest box) summed over all returns to the swarm. All the dances performed by each scout bee were for just one of the two nest boxes.

Descriptive statistics are reported as the mean \pm 1 s.d. To test for a difference in total signal strength between marked scouts from the 401 and 151 nest boxes, we used a mixed-model, repeated-measures ANOVA, which enabled us to check for nest box effects (fixed), swarm effects (random) and interactions. A repeated measures ANOVA was appropriate because for each swarm and

each nest box there were multiple bees producing data. To test for differences in the proportions of bees dancing, etc., between the marked scouts from the 401 and 151 nest boxes, we used χ^2 tests. Finally, to test for differences between the mean values of various measures for the marked scouts from the 401 or the 151 nest box (e.g. time spent inspecting the nest box, number of waggle runs produced after the first inspection of the nest box, etc.), we used *t*-tests when the data were normally distributed and Mann-Whitney *U*-tests when they were not.

RESULTS

Detailed records from one typical trial

Fig. 2 provides a detailed picture of the results obtained in one trial of the experiment. This trial, conducted on 17 July 2007, is representative of all seven trials. We see that the high-value (401) nest box was discovered first, shortly after 09:30 h, by a scout bee that was labeled Red soon after she arrived at the nest box. After inspecting the nest box for approximately 10 min, Red returned to the swarm cluster for a 6 min period. There she performed a vigorous dance containing 162 waggle runs, whereupon she returned to the 401 nest box, and so started a pattern of repeated trips between this nest box and the swarm cluster. We see, too, that shortly after Red performed her strong dance, other scout bees arrived at the 401 nest box and three of them (Orange, Yellow and Green) also performed a waggle dance for this nest box after spending 28–35 min there. One other scout bee, Blue, also spent considerable time (25 min) at the 401 nest box, but did not perform waggle dances at the swarm cluster. Finally, we see that at essentially the same time as scout bees were inspecting and responding to the high-value (401) nest box, other scout bees were inspecting and responding to the medium-value (151) nest box, though the six marked scouts from this nest box showed a weaker dance response. Only half of the scout bees (Yellow-White, Blue-White, and White-White) produced dance circuits, and they tended to perform fewer dance circuits per return to the swarm cluster than did the bees from the 401 nest box. By 12:00 h, all of the marked scout bees had stopped performing waggle dances upon return to the swarm cluster, and we concluded our recordings for this trial. Throughout the trial, each scout bee visited just one of the two nest boxes.

Comparison of dance responses for high- and medium-value sites

Fig. 3 provides a synoptic picture of the results obtained in all seven trials of the experiment. We see that there were notable differences

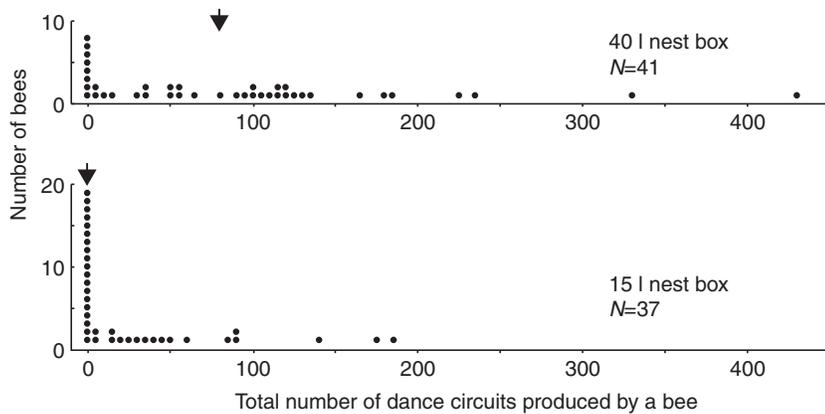


Fig. 3. Distributions of the number of dance circuits produced per scout bee, for bees reporting on either a 40 l (high value) nest box or a 15 l (medium value) nest box. The number shown for each bee is the sum of all dance circuits that she produced over her multiple returns to the swarm cluster. Black arrows indicate the median values for the two distributions.

between the scout bees from the high-value (40 l) and the medium-value (15 l) nest boxes in the total number of dance circuits produced per bee. Although there was great variation among the bees of each group, on average the dance circuit total per bee was higher for scouts from the 40 l nest box compared with those from the 15 l nest box: 89 ± 93 dance circuits vs 29 ± 49 dance circuits [repeated-measures ANOVA: $F_{1,66} = 10.52$, $P < 0.003$ (nest box); $F_{3,66} = 0.79$, $P > 0.50$ (swarm); $F_{3,66} = 0.23$, $P > 0.75$ (interaction)]. Also, fully 80% (33 of 41) of the scouts from the 40 l nest box produced dance circuits, whereas only 49% (18 of 37) of those from the 15 l nest box did so ($\chi^2 = 8.71$, $P < 0.004$).

These differences in the strength and likelihood of dancing between the two groups of scout bees do not reflect a difference in initial attention paid to the high-value and medium-value nest boxes. The two groups do not differ in the average time a bee spent at a nest box during her first visit there: scouts visited the 40 l box for 17.5 ± 8.3 min (range 5–37 min) vs 14.2 ± 10.0 min (range 2–40 min) for scouts visiting the 15 l box [repeated-measures ANOVA: $F_{1,66} = 1.66$, $P > 0.25$ (nest box); $F_{3,66} = 0.24$, $P > 0.75$ (swarm); $F_{3,66} = 0.79$, $P > 0.50$ (interaction)]. Nevertheless, the scout bees evidently judged the values of the two nest boxes differently during their first visits to these boxes, for upon their first returns to the swarm cluster, fully 76% (31 of 41) of the scouts from the 40 l nest box danced, whereas only 43% (16 of 37) of the scouts from the 15 l nest box did so ($\chi^2 = 8.51$, $P < 0.004$).

Rapid decay in dance response and visits to a site

We can see in Fig. 2 that the scout bees in the 17 July 2007 trial did not perform waggle dances each time they returned to the swarm cluster, but instead tended to do so only during their first few returns. This rapid decay in the dance response was typical. When we considered all 51 scout bees that performed dances within the seven trials of the experiment, we found that the average period during which a bee performed dances (i.e. the time interval from when she started her first dance to when she finished her last dance) was surprisingly short: scouts visiting the 40 l box, 28 ± 28 min (range 1–106 min); scouts visiting the 15 l box, 19 ± 20 min (range 1–60 min; $t_{49} = 1.27$, $P > 0.20$). Fig. 2 also shows that shortly after a bee's dance response decayed to zero, she ceased visiting the nest box. Considering again all 51 scouts that performed dances, we found that once a bee had made a return to the swarm without dancing, she made only 0.84 ± 0.87 additional visits to her nest box (range 0–3 visits). Evidently, as a bee's motivation to perform dances for a site decays away, so does her motivation to make visits to the site.

Fig. 4 shows that the decline in the dance responses of the scout bees followed a pattern of linear decay. Overall, we found that the

slope of the decay line was -17.2 dance circuits per return to the swarm (Fig. 4B). We also found, however, that the rate of this decay was not uniform among bees, with some bees letting their dancing decay rapidly over just one or two returns to the swarm, and others letting it decay more slowly over several returns to the swarm (Fig. 4A).

Strongest dance responses by discoverers of nest sites

An unexpected feature of how scout bees reported on the nest boxes was the way that the two bees in each trial that initially discovered the two nest boxes were more likely to perform dances than were the bees that subsequently visited the nest boxes (probably having been recruited to them). Over the seven trials, 86% (12 out of 14) of the 'initial scouts' performed a dance after their first visits to their finds, whereas only 55% (35 out of 64) of the 'subsequent scouts' did so after their first visits to a nest box ($\chi^2 = 4.62$, $P < 0.02$). Furthermore, the first reports made by the initial scouts tended to be longer than those made by the subsequent scouts. Among the 41 scouts that visited the 40 l nest box, the seven initial scouts produced 97.3 ± 66.9 dance circuits on their first returns to the swarm cluster, whereas the 34 subsequent scouts produced only 39.2 ± 43.6 dance circuits ($U_{[34,7]} = 176$, $P < 0.06$). Similarly, among the 37 scouts that visited the 15 l nest box, the seven initial scouts produced 43.0 ± 52.7 dance circuits on their first returns to the swarm cluster, whereas the 30 subsequent scouts produced only 14.3 ± 30.7 dance circuits ($U_{[30,7]} = 128$, $P < 0.40$).

Spatial precision of recruitment

The spatial precision that is possible in the recruitment of scout bees to a nest site was demonstrated by the set of events depicted in Fig. 2. On the morning of 17 July, the two nest boxes were 40 m apart at a distance of 240 m from the swarm cluster, so their angular separation from the swarm was only 10° . The nest boxes were mounted in identical lean-to shelters. Both shelters were positioned along the north side of a grassy road and both had their open sides facing south, i.e. toward the road. Consequently, the two nest boxes were matched in visibility. Shrubby vegetation lined the 40 m of roadside between the two nest boxes, so they could not be seen simultaneously, except from above. The two nest boxes were discovered nearly synchronously: 40 l nest box at 09:33, 15 l nest box at 09:39. Furthermore, the two scout bees that discovered these two nest boxes returned to the swarm cluster at about the same time: Red from the 40 l nest box at 09:44, and Red-White from the 15 l nest box at 09:41. However, only one bee performed a dance; Red produced 162 dance circuits in the time period 09:44–09:50. By 9:50, when Red's dance was finished, there was a clear difference

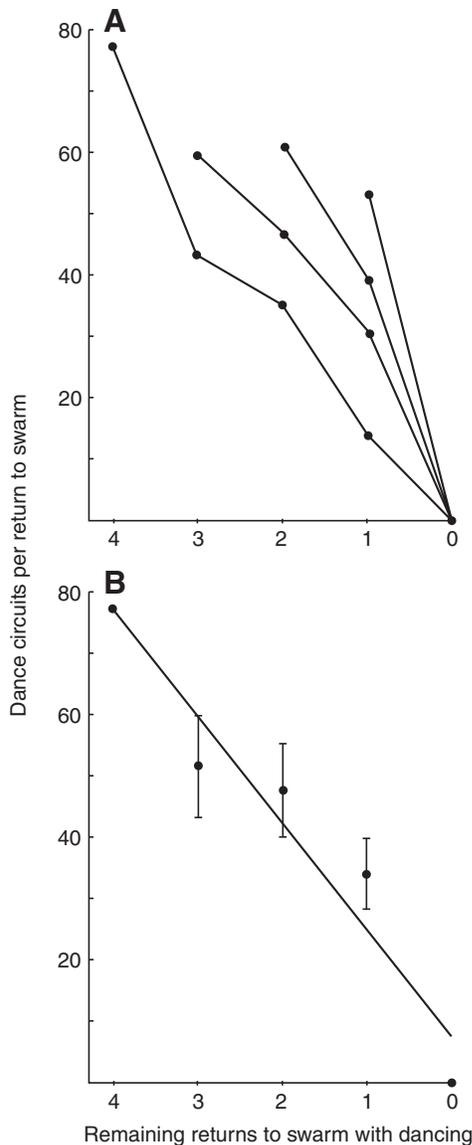


Fig. 4. Pattern of nest-site scouts performing shorter and shorter dances over consecutive returns to the swarm cluster. (A) Each line indicates the average pattern of reduced dancing for scout bees that danced during one, two, three or four consecutive returns to swarm. A total of 78 scout bees were observed, and 51 performed dances: 24 danced during just one return to the swarm, 11 danced during two returns, eight danced during three returns, seven danced during four returns, and one (not shown) danced during six returns. For an example of a bee producing increasingly shorter dances over four consecutive returns to the swarm, see the bee Orange (O) in Fig. 2. (B) Summary plot of the decay in dancing by nest-site scouts over consecutive returns to the swarm. Each data point represents the mean of the values shown in A; error bars represent ± 1 s.e.m. The overall rate of dance decay is -17.2 dance circuits per return to the swarm cluster.

in recruitment to the two nest boxes: 23 bees were counted outside the 40I nest box, whereas 0 bees were counted outside the 15I nest box.

DISCUSSION

A honeybee swarm is a decision-making unit, one that is capable of making a value-based choice as it selects its future home. To choose the nest site with the highest value from among the various

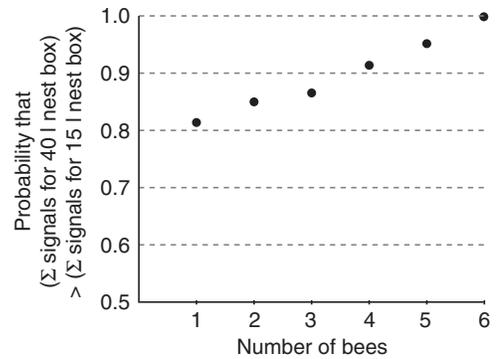


Fig. 5. The probability, for a given-size group of scout bees reporting on either the 40I nest box or the 15I nest box, that the total number of dance circuits (= signals) produced will be greater for the group reporting on the 40I nest box. Probabilities were calculated by taking 240 random samples from each of the two distributions of dance circuits per bee shown in Fig. 3. Next, the samples from each distribution were grouped consecutively into 240 groups of size 1, 120 groups of size 2, 80 groups of size 3, etc., and the dance circuits produced by the bees in each group were summed. Then, for each group size, the dance circuit totals were compared between matched pairs of groups (e.g. the first group of size 2 from the 40I distribution was paired with the first group of size 2 from the 15I distribution). In the 240 comparisons of group size 1, 81.4% of the groups reporting on the 40I nest box produced more dances; in the 120 comparisons of group size 2, 85.0% of the groups reporting on the 40I nest box produced more dance circuits; and so forth until in the 40 comparisons of group size 6, 100% of the groups reporting on the 40I nest box produced more dance circuits.

sites that it considers, a swarm must have a means for including information about site value in its sensory representation of the potential nest sites, i.e. the ensemble of waggle dances performed on the surface of a swarm. We have explored how the scout bees, which constitute the sensory apparatus of a swarm, scale the strength of their waggle dance signals in accordance with nest-site value and thereby code value in a swarm's sensory representation of the alternative dwelling places.

We have found that when a nest-site scout returns to her swarm and performs a waggle dance to report on the particular site that she has inspected, she adjusts the strength of her dancing as a function of the site's value: the higher the value of the site, the larger the number of dance circuits performed. We have also found that this coding of site value is extremely noisy across individuals, so that it is only on average that a higher-value site elicits a dance with more circuits (Fig. 3). Such noisiness is surprising, until one notes that in a swarm, as in a brain, the reporting of sensory information is spread over many units (bees or neurons). Consequently, even with much individual-level noise in the coding of value, there will be clear population-level differences in the total signaling for alternatives that differ in value. This fact is illustrated in Fig. 5, which shows how, as one sums the dance circuits performed by more and more bees, there is a rapid rise in the probability that the total amount of dancing for the 40I (better) nest box will exceed that for the 15I (poorer) nest box. Indeed, we see that if a swarm is presented with the two-alternative choice between the 40I and 15I nest box, it is extremely likely that its scouts will produce more dance circuits for, and so ultimately choose, the 40I nest box as long as the swarm has at least half a dozen scout bees reporting on each nest box.

The population-level coding of information about option value neatly solves the problem of noisy individual-level coding of this

information when there are multiple bees reporting on each option more or less simultaneously. However, at the start of the decision-making process, when the scouts are just starting to discover, inspect, and report on potential nest sites, there will be only a few bees reporting on each one and they will not be reporting simultaneously, so there will be much stochasticity in the sensory input to a swarm. Fig. 2 shows, for example, how for the first few hours of decision-making process of one typical swarm the scout bees' reports on the two experimental nest boxes varied greatly from one 5 min block to the next, with signaling for the 401 nest box only in some blocks, signaling for the 151 nest box only in other blocks, and no signaling for either nest box in many blocks. Given this high-level of sensory noise initially, even at the population level, it is not surprising that at first there is also much unpredictability in the evidence accumulation (build up of scouts) at the alternative nest sites [see for example, figure 2 in Visscher and Camazine (Visscher and Camazine, 1999) and figure 5 in Seeley and Buhrman (Seeley and Buhrman 2001)]. Swarms cope with this high noise initially in the evidence accumulation by having a high quorum threshold for choosing a site: 10–20 bees at the entrance to the site, or some correlate thereof (Seeley and Visscher, 2004; Passino and Seeley, 2006). This threshold is generally not reached until several hours have passed, by which time sizable populations of bees will be reporting on the various sites under consideration, hence there will be relatively low noise in the population-level coding of the values of the sites and thus low noise in the differential accumulation of evidence as a function of site value.

The potential for decision-making errors arising from the individual-level noise in the sensory coding is especially great when each site is first discovered by a scout bee, for if she fails to report it with a waggle dance, the site will be lost from the swarm's attention. A solution to this problem would be to have each scout bee that makes the initial discovery of a site likely to report on the site, thereby bringing it to the swarm's attention. Remarkably, the bees appear to do exactly this. We found that those scout bees that first visited the nest boxes in each trial almost always ($P=0.86$) performed dances upon return to the swarm, whereas the scouts that visited the same nest boxes subsequently (probably having been recruited to the boxes) were much less apt to dance ($P=0.55$). We do not know what gave these initial scouts an especially strong stimulus to dance. Perhaps it was each initial scout's experience of finding the site by herself (not having followed dances to find it) or of inspecting the site by herself (no encounters with other bees, no pheromones left by other bees, etc.). This 'discoverer-should-dance' solution is not foolproof, however. In a study of the decision-making ability of swarms (Seeley and Burhman, 2001), in which swarms were presented with a five-alternative choice (one 401 nest box and four 151 nest boxes), one swarm failed to choose the 401 option because the two scout bees that discovered it both failed to perform dances. Consequently, the swarm 'overlooked' the best alternative and chose one of the inferior ones.

We have shown that a scout bee codes the value of a potential nest site by adjusting the number of dance circuits that she produces to report the site (Fig. 3), but this may not be the full story. In his pioneering study of swarm decision making, Lindauer (Lindauer, 1955) stated that scouts reporting better sites appear to perform dances that are both *longer* and *livelier* than do scouts reporting poorer sites. Seeley and Buhrman (Seeley and Buhrman, 2001) checked Lindauer's observation by presenting a swarm with both an excellent (401) and a mediocre (151) nest box and video recording the dances of the scout bees for the two nest boxes, as they were performed side-by-side on the swarm cluster. (Note: they

did not follow individually marked bees, so they could not measure the total number of dance circuits that each bee produced over multiple bouts of dancing, as was done in the present study.) They found that, on average, the scout bees from the better nest box produced more dance circuits per return to the swarm. They also found that the bees increased the number of dance circuits per return to the swarm (C) by boosting both the duration (D , in seconds) and the rate (R , in circuits per second) of dance-circuit production (note that $C=D \times R$). Close analysis of the video recordings revealed that the scout bees adjusted R by changing the duration of the return-phase portion of each dance circuit, decreasing it to increase R . Evidently, it is this reduction in the return-phase time in the circuits of dances for better sites that gave Lindauer (Lindauer, 1955) the impression that dances for better sites are livelier. We strongly doubt, however, that adjusting R (dance liveliness) provides sensory coding in addition to what is accomplished by adjusting C (dance length). In a study of how bees report on food sources, it has been shown that nectar foragers adjust C as a function of food-source profitability, and that they do so by adjusting both D and R (Seeley et al., 2000), but that the difference in recruitment effectiveness between dances for a richer and a poorer food source is explained fully by the difference in number of circuits (C) in these dances (Seeley and Towne, 1992). We suspect that the same situation holds in reporting on nest sites: differences in recruitment to sites that differ in value are explained fully by differences in C between the dances representing the sites.

We have also confirmed previous reports (Lindauer, 1955; Seeley, 2003; Visscher, 2003) that nest-site scouts show decay in their dance response to a nest site, decreasing the number of dance circuits produced per return to the swarm cluster (Fig. 4). Seeley (Seeley, 2003) reported an average rate of dance decay of -15.7 dance circuits/return, and we found a very similar value: -17.2 dance circuits/return. Sensory receptor neurons often exhibit decay (adaptation) as a means of improving their ability to report stimulus changes (Shepherd, 1988; Young, 1989), but this is probably not the functional significance of the decay in dance response of nest-site scouts, since they are providing information about stimuli (potential nest sites) that are changing little, if at all. Their decay evidently serves instead to improve a swarm's decision-making ability, by limiting the amount of positive feedback that each bee generates in the build up of bees at her site and by limiting the number of visits that each bee makes to a site. A modeling study of the bees' decision-making process has shown that if there were no decay in the dance response, then a swarm's decision-making speed would increase but its accuracy would decrease; the swarm would be prone to making fast errors (Passino and Seeley, 2006). The decay of each scout bee's enthusiasm for her site also means that the competitive process of accumulating bees committed to different sites is 'leaky'; shortly after a bee ceases dancing for a site she also ceases visiting the site. Leakage in the accumulation of evidence is a key feature of several models developed in mathematical psychology to model the neurobiology of decision making [e.g. the leaky competing accumulator model of Usher and McClelland (Usher and McClelland, 2001)]. In these models, leakage seems to improve decision making by increasing the time over which noisy evidence accumulates until sufficient information for a decision is obtained, i.e. leakage in the accumulation process helps prevent fast errors.

In closing, it should be noted that a swarm's ability to build a useful sensory representation of the alternative nest sites depends critically on each scout bee tightly coupling her information about the value of a site and with her information about the location when

she produces her waggle dances. Unless each scout bee makes location-specific signals of value, a swarm will be unable to generate adaptively differential accumulations of decision evidence (scout bees) at the different sites, and so achieve the decision transformation (Fig. 1). It has long been known how nest-site scouts code site location in their dances (Lindauer, 1955), and this report now makes it clear how they code site value. And because we know that each nest-site scout visits and performs dances for just one site at a time (Seeley and Buhrman, 1999) (see also the records of individual bees in Fig. 2), we can be confident that there is a tight coupling of value information and location information in their dances. Although unintended, the bees gave us an impressive demonstration of just how effective this value-location coupling is when, on the morning of July 17, the scout bee Red performed a dance indicating the location of a high value site (the 401 nest box), and this stimulated a rapid buildup of scout bees at the 401 nest box, but not at the 151 nest box just 40 m (10°) away!

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