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ORIGINAL ARTICLE

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Nest-site selection in honey bees: how well do swarms implement the "best-of-*N*" decision rule?

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Abstract This study views a honey bee swarm as a supraorganismal entity which has been shaped by natural selection to be skilled at choosing a future home site. Prior studies of this decision-making process indicate that swarms attempt to use the best-of-*N* decision rule: sample some number (*N*) of alternatives and then select the best one. We tested how well swarms implement this decision rule by presenting them with an array of five nest boxes, only one of which was a high-quality (desirable) nest site; the other four were medium-quality (acceptable) sites. We found that swarms are reasonably good at carrying out the best-of-*N* decision rule: in four out of five trials, swarms selected the best site. In addition, we gained insights into how a swarm implements this decision rule. We found that when a scout bee returns to the swarm cluster and advertises a potential nest site with a waggle dance, she tunes the strength of her dance in relation to the quality of her site: the better the site, the stronger the dance. A dancing bee tunes her dance strength by adjusting the number of waggle-runs/dance, and she adjusts the number of waggle-runs/dance by changing both the *duration* and the *rate* of her waggle-run production. Moreover, we found that a dancing bee changes the rate of her waggle-run production by changing the mean duration of the return-phase portion of her dance circuits. Differences in return-phase duration underlie the impression that dances differ in liveliness. Although a honey bee swarm has bounded rationality (e.g., it lacks complete knowledge of the possible nesting sites), through its capacity for parallel processing it can choose a nest site without greatly reducing either the breadth or depth of its consideration of the alternative sites. Such thoroughness of information gathering and processing no doubt helps a swarm implement the best-of-*N* decision rule.

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Introduction

Multilevel selection theory shows that groups of organisms can evolve high levels of functional organization when between-group selection prevails over within-group selection (Williams 1992; Bourke and Franks 1995; Sober and Wilson 1997). The strongest empirical evidence that natural selection has actually produced adaptive units at the group level comes from the biology of social insects. Here we find striking examples of groups (colonies) functioning as coherent wholes in which the members contribute harmoniously to the goal of propagating the group's genes. Moreover, the members of these colonies possess morphological, physiological, and behavioral specializations that serve the efficient functioning of the colony to which they belong. The best examples are the colonies of such social insects as leaf-cutter ants (Hölldobler and Wilson 1990), fungus-growing termites (Lüscher 1955), and honey bees (Seeley 1995).

In honey bees, what appears to be an impressive example of a colony behaving as a supraorganismal entity is the way in which a swarm of bees chooses its future home. The members of a swarm work together to discover several potential nesting cavities, evaluate each one, choose among them, and finally move en masse to the chosen site. Indeed, swarms have been described as "higher-order cognitive entities" (Markl 1985) and "collective brains" (Holmes 1999). However, just how well a honey bee swarm functions as a collective decision-making agent remains unknown. To address this issue, and so clarify the degree to which a honey bee swarm is a supraorganismal entity, we have tested how well swarms choose their nest sites.

Decision making is a process whereby a course of action is chosen from a number of alternatives. In choosing among several home sites, a swarm faces a decision-making problem akin to that which a human faces in choosing among several versions of a consumer item. This "consumer-choice problem" (Martin and Moon 1992) is similar, but not identical, to the mate-choice problem that has already attracted much attention from behavioral ecologists (Janetos 1980; Parker 1983; Real 1990, 1991; Getty 1996). Prior studies of the process of nest-site selection in honey bees (Lindauer 1955, 1961; Camazine et al. 1999; Seeley and Buhrman 1999) indicate that the parameters of a swarm's decision-making problem are as follows: (1) the number, quality variation, and encounter order of the alternatives are unknown at the outset; (2) the alternatives are not ephemeral, hence the choice can involve choosing the best in a set of simultaneously considered options, and (3) the search for alternatives has costs, but the marginal cost of locating additional alternatives is low. Given these parameters, especially the low marginal cost of searching (Lippman and McCall 1976; Real 1990), it is not surprising that a honey bee swarm employs the best-of-*N* decision rule: a swarm samples some number (*N*) of alternative sites and then tries to select the best one for its future home (Lindauer 1955; Seeley 1977). But whether or not swarms are actually good at selecting the best of the *N* alternatives has, until now, not been rigorously tested. We have done so by performing an experiment in which swarms had to choose from a controlled array of nest boxes, only one of which was a high-quality nest site; the others were of medium quality. We found that swarms are good, but not perfect, at implementing the best-of-*N* decision rule. We also made important findings about the behavioral mechanisms that underlie a swarm's ability to function as a skilled decision maker.

Methods

General plan of study

We tested the decision-making abilities of swarms by presenting them with a choice among five nest boxes: one of high quality and four of medium quality. To ensure that each swarm's decision-making task was non-trivial, we made sure that each nest box was an acceptable nest site. (Had we not done this, and we had presented each swarm with one acceptable and four unacceptable nest boxes, the test would not have challenged them.) Therefore, our study required a preliminary experiment, using a two-nest-box array, to determine how to configure a nest box so that it is an acceptable, but not high-quality nest site – what we call a "medium-quality" site. We assayed a swarm's interest in each nest box throughout the decision-making process by counting the scout bees at each nest box. These counts revealed which sites were discovered, the order of their discovery, the level of interest in each site, and which site was ultimately chosen. We also videorecorded the dances of bees advertising high-quality and medium-quality sites to see how bees adjust their waggle-dance production in relation to nest-site quality.

The two-nest-box experiment

We knew from previous studies (Seeley 1977; Seeley and Morse 1978) two important variables assessed by bees evaluating a cavity as a potential dwelling place: cavity volume and entrance size. We also knew the bees' preferences regarding these variables, and so could create high- and low-quality nest boxes. In general, bees prefer larger rather than smaller cavities (i.e., 40- over 10-l ones) and smaller rather than larger entrances (i.e., 15- over 75-cm^2 ones). But we did not know how exactly to make a medium-quality nest box. To solve this puzzle, we presented the bees with nest boxes in which volume and nest entrance were varied and observed how the desirability of a given nest box changed when these properties were changed.

Study site

The experiment was conducted at the Shoals Marine Laboratory on Appledore Island, Maine (42°58′ N, 70°37′ W). Because this 39-ha island is nearly treeless and bears only a few buildings, it has few natural nest sites for honey bees. Here we could set out our experimental nest boxes and be confident that they would get the attention of the scout bees from our swarms.

Swarm preparation

All our swarms were artificial swarms prepared from colonies kept on the mainland. These colonies were headed by "Buckfast" queens (Adam 1987). In making an artificial swarm, we first located a colony's queen and put her in a small cage (3.2×10×1.6 cm). Then, using a large funnel, we shook 1.0 kg of worker bees (some 7,500 bees; Mitchell 1970) from the frames of this colony's hive into a swarm cage (15×25×35 cm) made of wood with wire screen sides. We also placed the caged queen inside the swarm cage. The caged bees were then ferried to Appledore and kept in the shade for 24–72 h (until copious wax scales appeared beneath the swarm cage). During this time, we fed the bees ad libitum with 2.0 mol/l sugar water. Finally, the swarm cage was opened, the queen (still in her own little cage) was fastened to a swarm mount (see below), and the workers were shaken onto the base of the mount. Within an hour, the workers were clustered around the queen and behaving like a natural swarm.

Apparatus

Swarms were placed on a swarm mount that has been described previously (see Fig. 1; Seeley and Buhrman 1999). This facilitated videorecording the scouts' dances to compare those representing high- and medium-quality sites (see Video analysis section, below). The nest box design is shown in Fig. 1. Each was built of 1.9-cm-thick plywood and varnished on the outside. The volume of each nest box was 40 l, but this could be reduced to 20, 15, or 10 l by installing an inner wall in one of the positions shown in Fig. 1. The entrance to each nest box was 120 cm^2, but this could be reduced to 60, 30, or 15 cm^2 by installing one of the entrance reducers shown in Fig. 1. All the nest boxes were housed in opensided shelters (see Fig. 1) to equalize their exposures.

Experimental layout and data collection

Each trial began by placing a swarm on the mount located on a covered porch. While on the mount, the swarm was fed ad libitum with sugar water from two feeder bottles. Two nest boxes were placed in different directions from the swarm but at the same distance (250 m) and with their entrances facing the same direction (south; see Fig. 2). To help scouts locate the nest boxes, we pinned a pheromonal swarm lure (Ecogen, Langhorne, Pa.) inside each one at the start of a trial. We then monitored the swarm cluster for bees performing waggle dances. If a bee danced for a site other than one of the nest boxes, we removed her. Once a bee began dancing for one of the nest boxes, the person making the scout bee counts ran to the nest boxes to remove the swarm lures and begin making counts. Meanwhile another individual continued censoring the swarm of news of sites other than our nest boxes. In most

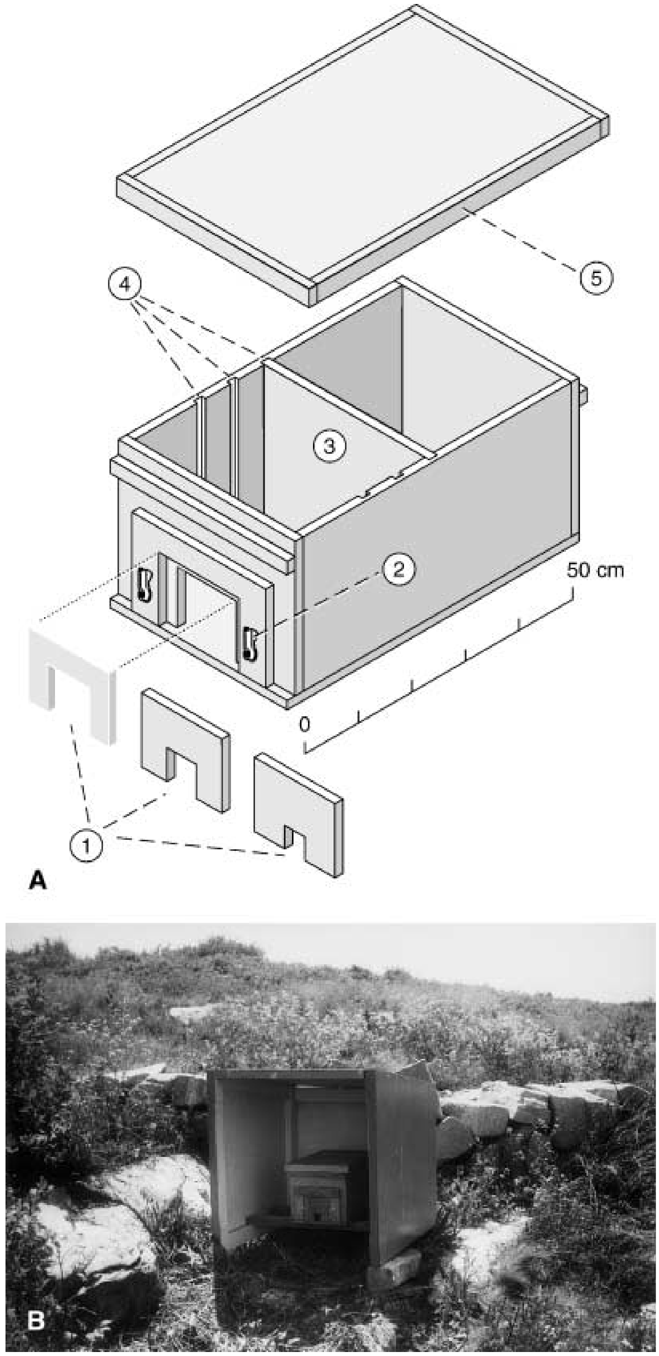


Fig. 1 Design of nest box (**A**) and of nest box shelter (**B**): *1* entrance reducers (with 60-, 30-, and 15-cm^2 entrance openings); *2* turn buttons to hold the entrance reducers in place; *3* the movable inner wall that determines the nest cavity volume (10, 15, or 20 l with it inserted, and 40 l with it removed); *4* grooves for holding the inner wall in place; *5* light-proof lid

cases, once a scout discovered and began dancing for one nest box, other scouts (probably errant recruits) soon appeared at the adjacent nest box. We continued counting bees at the nest boxes, censoring dances at the swarm, and occasionally varying the volume or entrance size of each nest box, until the swarm lifted off to fly to one of the boxes. No swarm actually reached its chosen site because its caged queen remained behind at the swarm mount.

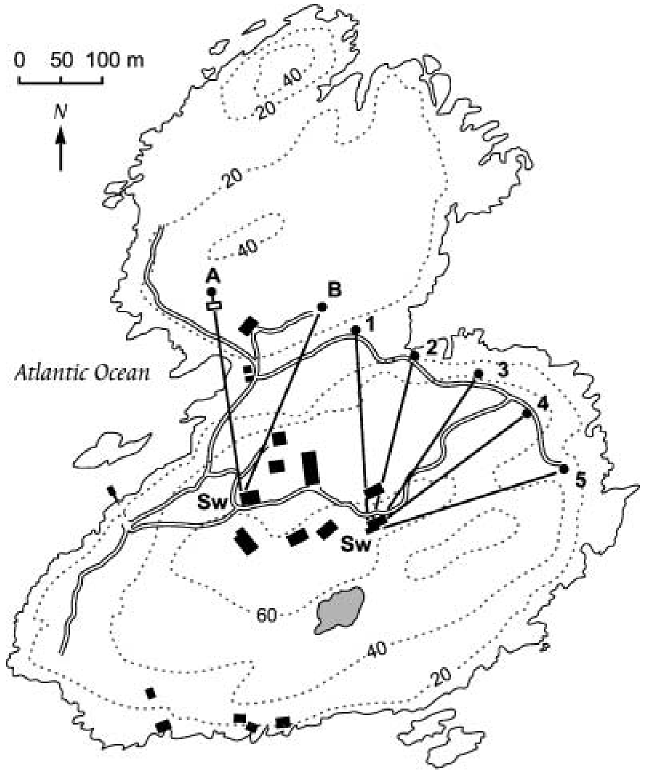


Fig. 2 Layouts on Appledore Island. For the two-nest-box experiments, the swarm (*Sw*) was mounted on the porch of Laighton House while the nest boxes were positioned at sites *A* and *B*. For the five-nest-box experiments, the swarm (*Sw*) was mounted on the porch of Bartel's Hall while the nest boxes were positioned at sites *1–5*. *Contour lines* indicate feet above sea level

Our protocol for counting bees at the nest boxes was as follows. One person walked between the nest boxes, visiting each one every 6 min, thereby surveying both nest boxes on a 12-min cycle. While at a nest box, the counter sat 3 m in front of it and over a 3-min period made five counts of the maximum number of bees seen simultaneously at the nest box (either flying around it or crawling upon it) during a 30-s period.

The five-nest-box experiment

The materials and methods for this experiment were the same as for the two-nest-box experiment except that (1) we used a five-nest-box array (see Fig. 2) in which each nest box faced east; (2) after trial 1 we did not use pheromone lures, and (3) when counting the scout bees, the counter surveyed all the nest boxes on a 30-min cycle instead of a 12-min cycle. Five trials were performed and each of the five sites in the array served as the high-quality site in one trial. One of us (T.D.S.) used a random number table to determine the order in which the different sites would serve as the high-quality site and withheld this information from the individuals making the scout bee counts. Thus the scout bee counts were made blindly with respect to nest-site quality.

The video analysis

To test the hypothesis that a scout bee advertising a nest site adjusts waggle-dance strength in relation to nest-site quality, we examined videorecordings made in the last two trials of the two-nest-box experiment. This enabled us to compare dances for a medium- and for a high-quality site. Note, these recordings

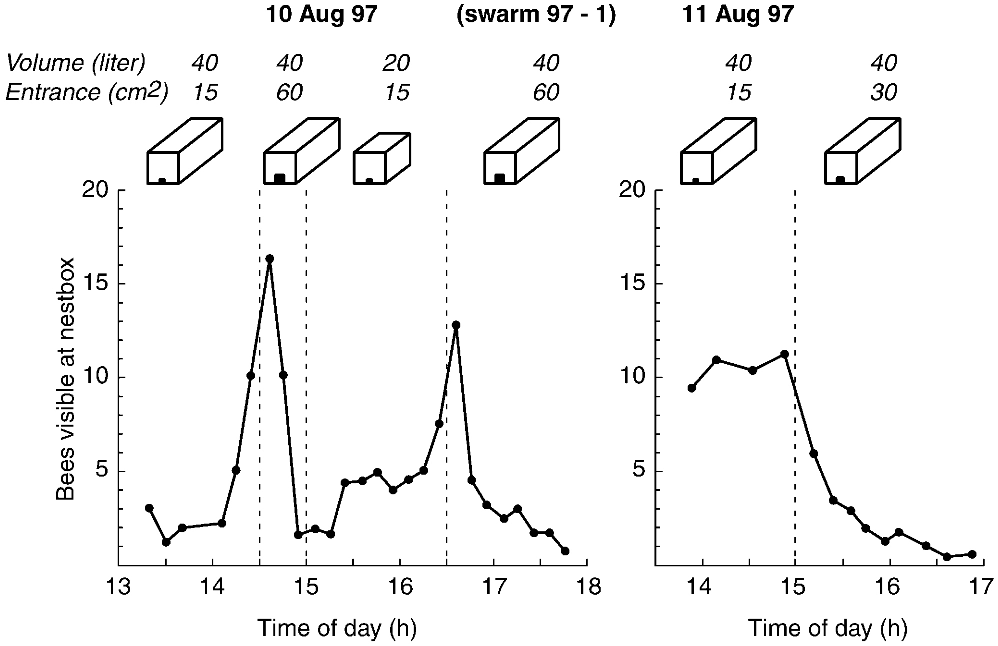


Fig. 3 Results of an experiment to determine the properties of a medium-quality nest site, one that is acceptable but not desirable. We monitored the swarm's response to a nest box at various settings of cavity volume and entrance size; *dashed vertical lines* show when the box settings were changed. We monitored the swarm's response by counting the bees visible at the nest box

enabled us to compare dances that were performed by bees from the *same colony* at the *same time* and in the *same place*, since the dances for both sites were performed side-by-side on a swarm. Furthermore, because we switched the locations of the high- and medium-quality sites during each trial, we unlinked nest-site quality from nest-site location and from scout-bee group. Thus we are confident that any differences found between dances for high- and medium-quality sites must reflect the difference in site quality rather than a difference in some extraneous variable.

Apparatus

Video equipment was a camera (Panasonic WV-F250B) and videocassette recorder (Panasonic AG-7450) equipped with a time-code generator (Panasonic AG-F745). The videotapes were analyzed using a videocassette player with variable-speed playback (JVC BR-S525U).

Data analysis

For each dance, we determined the starting time, ending time, total number of waggle runs, and angle of waggle runs. We judged a bee's dance to have ended when she either stopped dancing for more than 4 s or flew from the swarm. We measured the waggle-run angle of each dance to establish which nest site it represented. We assessed the liveliness of each dance and assigned each dance to one of three categories: lively, moderate, and sluggish. To identify an objective behavioral variable associated with our subjective assessments of liveliness, we examined the videorecords of the first 10 lively dances and the first 10 sluggish dances performed in each trial. These 20 dances were chosen blindly with respect to the nest sites they represented. We focused on the first five circuits of each dance and determined for each circuit the durations of its waggle and return phases (see Fig. 92 in von Frisch 1967). We did so by counting the number of video frames in each phase; the videocamera operates at 30 frames/s so our precision was 0.033 s.

All numerical results are given as the mean±1 SD. Statistical tests of the difference between two means were performed using Student's *t*-test or the Mann-Whitney *U*-test (used to compare the mean values of return-phase duration, since these data were not normally distributed). We also used the χ^2-test in a contingency table analysis of the independence of waggle-dance liveliness and nest-site quality.

Results

The two-nest-box experiment: how do we make a mediocre nest site?

Swarm 97-1

This swarm was placed on the swarm mount at 1400 hours on 9 August 1997, and the nest boxes at both sites A and B were set up with a cavity volume of 40 l and an entrance opening of 15 cm^2 (hereafter refered to as "40/15 settings"). The next day, at 1216 hours, a bee was seen dancing for nest box B and a check of the nest boxes revealed two scout bees at site B but none at site A. By 1300 hours, several bees were performing dances for nest box B but still no bees were visiting nest box A, so we closed nest box A and concentrated on nest box B for the rest of the afternoon and throughout the following day.

Figure 3 depicts the results obtained with this swarm. Initially, the nest box was given 40/15 settings and the number of bees visible at it rose to a high level, more than 15 bees. Then, at 1430 hours, the settings for this nest box were switched to 40/60, whereupon the number of bees plummeted. To prevent total abandonment, at 1500 hours we changed the settings to 20/15. The number of bees gradually began to increase and was again approaching a high level at 1630 hours when the nest box was once more given 40/60 settings. As before, the number of bees fell precipitously and by 1800 hours, the nest box was nearly without bees. We began the next day by giving the nest box 40/15 settings, to make it attractive, but rainy weather in the morning prevented the bees from becoming active until the afternoon. By 1500 hours the number of bees had again risen to a high level, but when the nest box settings were changed to 40/30 at 1500 hours, the number quickly declined.

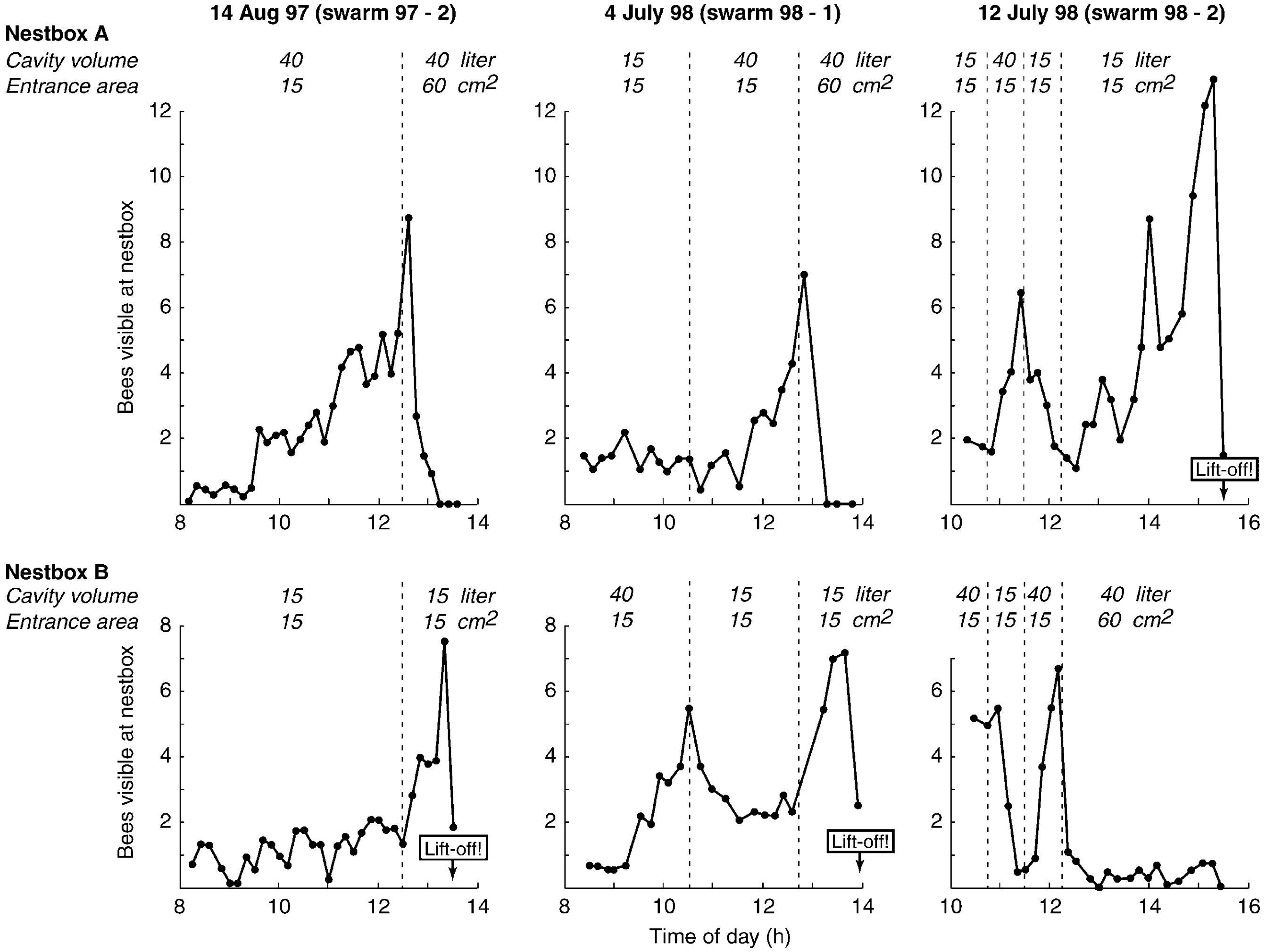


Fig. 4 Results of three trials of an experiment designed to determine the properties of a medium-quality nest site. Figure format follows that of Fig. 3

These results revealed that the bees judged a nest box with 40/15 settings to be a high-quality nest site (as expected) and that they judged a nest box with settings of 40/30 or 40/60 to be a low-quality, probably even unacceptable, nest site. With disappointment, we concluded it unlikely that we could create medium-quality nest sites by giving our nest boxes entrance openings of 30 or 60 cm^2. Fortunately, however, these results also hinted that we might be able to create a medium-quality site by reducing the cavity volume, for although the counts had risen when the nest box was given 20/15 settings, we sensed they had not risen as quickly with the 20/15 as with the 40/15 settings. We pursued this lead by testing a swarm with 40/15 and 15/15 nest boxes.

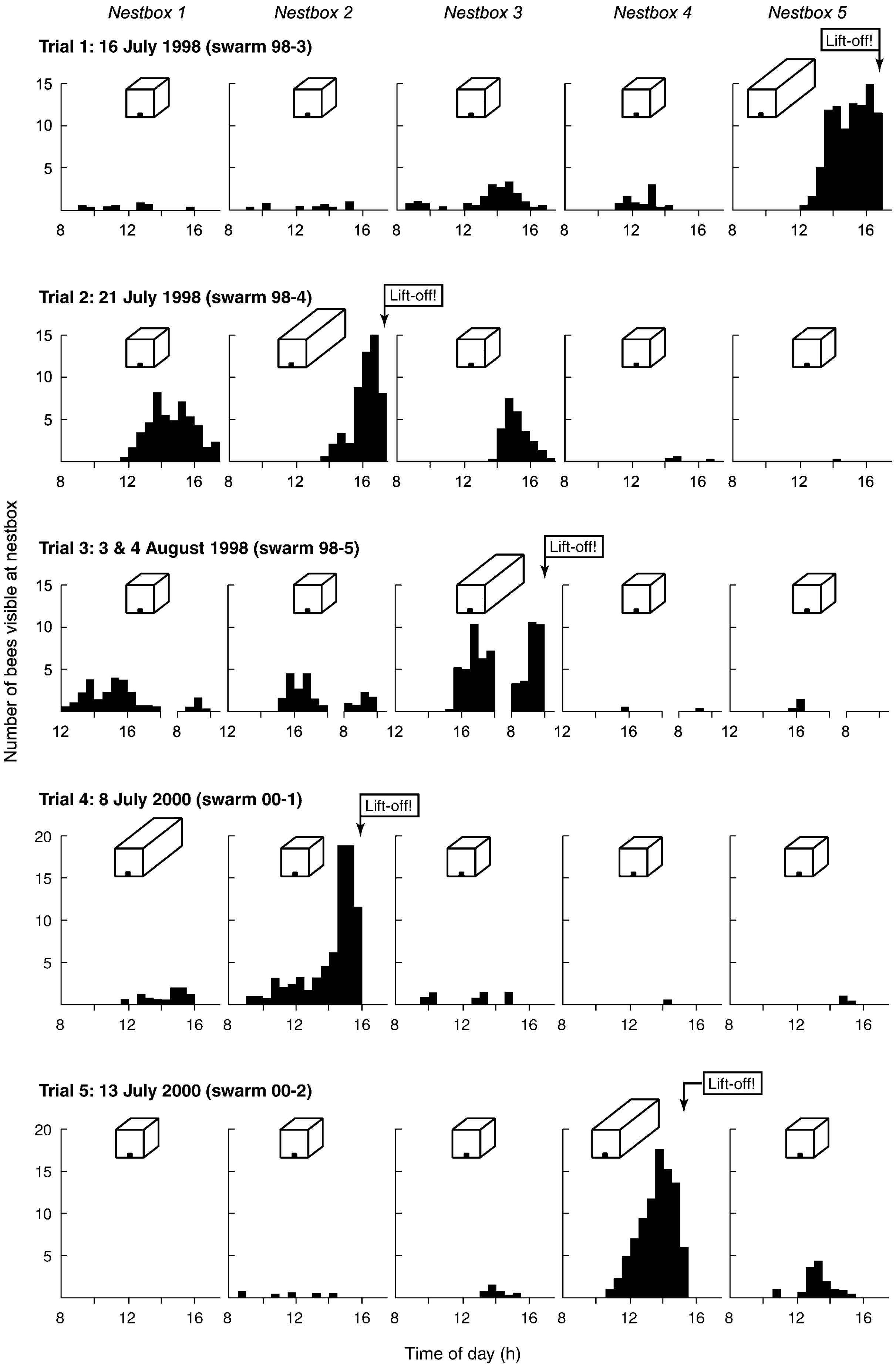
Swarm 97-2

This swarm was placed on the swarm mount at 1200 hours on 13 August 97 and the nest boxes at sites A and B were given settings of 40/15 and 15/15, respectively. A bee was seen dancing for nest box A at 1641 hours and by 1800 hours both nest boxes were being scouted.

Figure 4 depicts the results obtained the next day. In the morning, the number of bees visible at nest box A rose slowly but steadily, reaching nine bees by early afternoon. Meanwhile, the number at nest box B stayed low at just one to two bees. Evidently, the swarm was treating nest box A as a high-quality site. But was it also treating nest box B as a medium-quality site, that is, one not highly desirable but certainly acceptable? To see if the swarm would accept nest box B, at 1230 hours we changed the settings of nest box A to 40/60. Immediately, the number of bees at nest box A plunged and the number at nest box B began climbing to a high level. Within an hour, at 1328 hours, the swarm lifted off and flew toward nest box B.

This swarm clearly preferred nest box A with its 40/15 settings over nest box B with its 15/15 settings, and there is no doubt that ultimately the swarm would

Fig. 5 Results of five trials of the five-nest-box experiment in which we presented a swarm with a choice among four medium-quality nest sites (15-l cavity and 15-cm^2 entrance) and one high-quality nest site (40-l cavity and 15-cm^2 entrance) ▶



Trial 1: 16 July 1998 (swarm 98-3)

Trial 2: 21 July 1998 (swarm 98-4)

Trial 3: 3 & 4 August 1998 (swarm 98-5)

Trial 4: 8 July 2000 (swarm 00-1)

Trial 5: 13 July 2000 (swarm 00-2)

have chosen nest box A if we had not degraded it by enlarging its entrance. It is also clear that this swarm, when faced with a choice between two nest boxes, one with 40/60 settings and one with 15/15 settings, preferred and eventually adopted the latter. Taken together, these results indicate that our swarm responded to nest box B with its 15/15 settings as a mediocre, yet acceptable, nest site.

Swarms 98-1 and 98-2

As shown in Fig. 4, these two swarms responded to our nest boxes in ways similar to swarm 97-2. Both swarms showed a preference for a 40/15 over a 15/15 nest box, but when presented with a choice between a 40/60 and a 15/15 nest box, they preferred and eventually adopted the 15/15 nest box.

Conclusion

We conclude that a nest box with a 15-l cavity and a 15-cm^2 entrance is a medium-quality nest site, i.e., one that is not ideal but is acceptable to the bees. In all three trials in which we offered a 15/15 and a 40/15 nest box, the swarm preferred the 40/15 nest box. But at the end of each trial, when the 40/15 nest box was degraded by converting it to a 40/60 nest box, the swarm accepted the 15/15 nest box as its future dwelling place. Our conclusion that a 15/15 nest box is a medium-quality site is further supported by our findings on the dances for the nest boxes (see Video analysis, below). Specifically, we observed that bees performed waggle dances for the 15/15 nest box (implying that it was acceptable), but that these dances were not as strong as those performed for the 40/15 nest box (implying that the 15/15 nest box was less desirable than the 40/15 one).

The five-nest-box experiment: how well does a swarm choose the best site?

Trial 1: swarm 98-3

As shown in Fig. 5, scouts were seen first at nest box 3 (at 0843 hours), and shortly thereafter at nest box 1 (at 0902 hours) and nest box 2 (at 0908 hours). For the next 3 h there was little dancing on the swarm and the mean number of bees visible at nest boxes 1–3 never rose above one bee. At 1117 hours, the first scout was seen at nest box 4. At 1226 hours, the first scout was seen at nest box 5. At 1306 hours, a vigorous dancer for nest box 5 was recorded. During the afternoon, all of the medium-quality sites continued to be visited by a few bees, and at nest box 3 the mean number of bees rose to about three before starting to taper off at 1500 hours. But at the high-quality site, nest box 5, the number of bees rose rapidly between 1200 and 1500 hours and remained at a high level until 1650 hours, when the swarm lifted off and flew toward nest box 5.

Thus in the first trial, the swarm chose the best site even though all the medium-quality sites had been found earlier and so had a head start in attracting the bees. Indeed, the bees found one of the medium-quality sites (nest box 3) nearly 4 h before finding the high-quality site.

Trial 2: swarm 98-4

As shown in Fig. 5, in this trial the swarm also chose the best site. This time the high-quality site was not the last to be discovered but its choice was still remarkable. By the time the high-quality site (nest box 2) was discovered, a large number of bees were visiting nest box 1, and yet nest box 2 won the competition for the scouts' attention.

Trial 3: swarm 98-5

As shown in Fig. 5, in this trial, as in the previous two, the swarm discovered all five nest boxes and managed to select the high-quality one for its future home. Note that in this trial, the swarm chose the high-quality site even though it found this site (nest box 3) some 4 h after it found one of the medium-quality sites (nest box 1).

Trial 4: swarm 00-1

As shown in Fig. 5, in this trial, the swarm chose one of the medium-quality sites, nest box 2. Although this was the first nest box discovered (on 7 July), it is unlikely that this gave it a lead in the competition for scouts, for by the end of the first day, fewer bees were seen at nest box 2 than at nest box 3. For some unknown reason on the next day, 8 July, there was little dancing by scouts visiting a site other than nest box 2, even by those visiting the high-quality site (nest box 1)! Hence nest box 2 easily won the competition for the scouts' attention.

Trial 5: swarm 00-2

As shown in Fig. 5, the swarm in this trial chose the best site in a straightforward manner. Even though the swarm discovered three medium-quality sites along with the high-quality site, and even though one of the medium-quality sites was found 2 h before the high-quality site, only the high-quality site was recruited to persistently and strongly. Consequently, in this trial, the high-quality site garnered most of the scout bees' interest.

Conclusion

We conclude that the decision-making process worked reasonably well in these swarms. In four out of five

Table 1 Total amount, duration, and rate of waggle-run production in relation to nest-site quality

	Swarm 98-1: 4 July 1998			Swarm 98-2: 12 July 1998		
	0830–1030 hours: 1045–1245 hours:	site A 15 l site A 40 l	site B 40 l site B 15 l	1100–1130 hours: 1145–1215 hours:	site A 40 l site A 15 l	site B 15 l site B 40 l
Dance variable	40-l nest box	15-l nest box	*P*	40-l nest box	15-l nest box	*P*
Waggle-runs/dance	37.5±27.7	14.2±11.1	<0.005	34.8±28.2	13.3±11.0	<0.009
Seconds/dance	84.6±47.2	45.8±29.6	<0.008	87.3±59.4	44.4±35.5	<0.015
Waggle-runs/s	0.44	0.31		0.40	0.30	
n	43	13		37	15	

cases, the swarm chose the best site from a set of five acceptable sites. This outcome is quite unlikely to have occurred simply by chance, i.e., if the swarms had made random choices [$P=0.0064$; calculated as the binomial probability of getting 4 "heads" and 1 "tails" where p=the probability of getting a "heads" (choosing the one high-quality site)=0.2 and q=the probability of getting a "tails" (choosing one of the four medium-quality sites)=0.8]. How did the swarms achieve such accurate decision making? To begin to address this question, we consider how a scout bee tunes waggle-dance strength to nest-site quality.

Video analysis: how does a scout tune her dancing to site quality?

In the first three trials of the five-nest-box experiment, we noticed a slower buildup at the medium-quality nest boxes than at the high-quality one (see Fig. 5). This difference suggested that a scout adjusts the strength of her waggle dance in accordance with the quality of her nest site. To compare dances for high- and medium-quality sites, we videorecorded the dances performed with swarms 98-1 (trial 3) and 98-2 (trial 4) in the two-nest-box experiment. With swarm 98-1, we videorecorded the dances for 2 h when nest box A had 40/15 settings and nest box B had 15/15 settings, and 2 h when the settings were reversed (see Table 1, Fig. 4). With swarm 98-2, we videorecorded the bees' dances for 30 min when nest box A had 40/15 settings and nest box B had 15/15 settings, and 30 min when the settings were reversed. With both swarms, we did not record dances for 15 min after reversing the settings, to let the bees adjust to the new settings.

As shown in Table 1, the bees of swarm 98-1 performed 43 dances for the high-quality nest box and 13 dances for the medium-quality one, while the bees of swarm 98-2 performed 37 and 15 dances, respectively. Note too that for both swarms, the number of waggle runs/dance was nearly three times greater for the high-quality than for the medium-quality site. Clearly, the scouts adjusted dance strength in relation to site quality, but how exactly did they do this? The number of waggle runs/dance is the product of the *duration* of dancing and the *rate* of waggle-run production while dancing. Do scouts adjust both duration and rate of waggle-run production?

Adjustment of dance duration

In both swarms, dances for the high-quality site lasted significantly longer, approximately twice as long, as dances for the medium-quality site (Table 1). Clearly, the scouts adjusted the duration of waggle-run production in relation to nest-site quality.

Adjustment of dance rate

Table 1 shows that dances for high-quality and medium-quality sites differed more strongly when compared in terms of waggle runs/dance than in terms of seconds/dance. Evidently, when advertising the high-quality nest site relative to advertising the medium-quality one, scouts not only danced longer but also produced waggle runs at a higher rate. Indeed, in swarms 98-1 and 98-2, bees dancing for the high-quality site produced waggle runs at rates of 0.44 and 0.40 waggle runs/s on average, whereas bees dancing for the medium-quality site produced waggle runs at rates of just 0.31 and 0.30 waggle runs/s ($P<0.05$).

Analysis of dance liveliness

Adjustment of the rate of waggle-run production in relation to nest-site quality may underlie the observation that waggle-dance liveliness is correlated with nest-site quality (Lindauer 1955). To test this idea, we rated the liveliness of each dance that we videorecorded with swarms 98-1 and 98-2 using a three-level scale: lively, moderate, or sluggish. Ratings were assigned blindly, i.e., without knowing the quality of the site represented by a dance.

Was waggle-dance liveliness a function of nest-site quality? Evidently it was. Table 2 shows for both swarms the distributions of lively, moderate, and sluggish dances for the high-quality (40-l) and medium-quality (15-l) nest sites. For both swarms, most of the dances for the high-quality site were lively or moderate, whereas most of those for the medium-quality site were moderate or sluggish. Statistical analysis revealed a significant ($P<0.05$ or 0.025) association between site quality and dance liveliness.

How do scouts alter their dance liveliness? It seemed to us that lively dancers, but not sluggish ones, were

Table 2 Waggle-dance liveliness in relation to nest-site quality

Dance liveliness	Swarm 98-1: 4 July 1998		Swarm 98-2: 12 July 1998	
	40-l nest box	15-l nest box	40-l nest box	15-l nest box
Lively	21	2	15	1
Moderate	12	4	16	7
Sluggish	10	7	6	7
P	<0.05		<0.025	

Table 3 Comparisons of waggle-phase and return-phase duration between dances of different liveliness

Dance liveliness	Swarm 98-1: 4 July 1998		Swarm 98-2: 12 July 1998	
	Waggle-phase (s)	Return-phase (s)	Waggle-phase (s)	Return-phase (s)
Lively	0.59±0.12	1.18±0.30	0.65±0.12	1.20±0.13
Sluggish	0.61±0.17	2.07±0.47	0.61±0.06	2.28±0.43
P	>0.50	<0.001	>0.25	<0.001

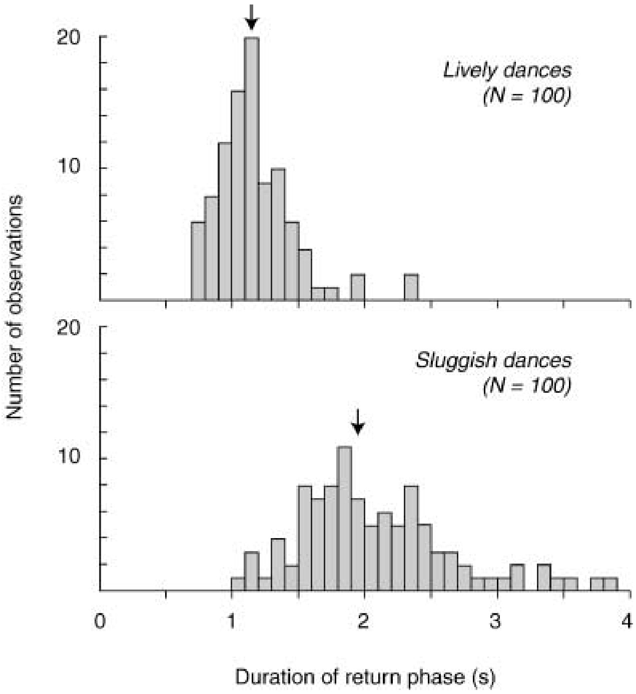


Fig. 6 Distributions of return-phase duration in lively and sluggish waggle dances. *Arrows* indicate median values. The mean values of the two distributions (1.19 s and 2.18 s) differ markedly, as do the distributions overall ($P<0.001$)

“bursting” with desire to produce waggle runs, because immediately upon finishing one waggle run they whirled around to start the next. In other words, lively dancers seemed to spend less time between waggle runs than did sluggish dancers. To test this idea, we determined the mean waggle-phase duration and the mean return-phase duration for the first ten lively dances and the first ten sluggish dances for both swarms 98-1 and 98-2. As shown in Table 3, in both swarms we found no difference in waggle-phase duration between lively and sluggish dances, but we found a substantial difference in return-phase duration. Specifically, the mean return-phase duration of sluggish dances was nearly twice that of lively dances.

One might wonder if the difference in mean return-phase duration between lively and sluggish dances arose because sluggish dancers *typically move slightly more slowly* during their return phases, or if it is because they *occasionally move much more slowly* during their return phases. These two possibilities were resolved by examining the distributions of return-phase duration for lively and sluggish dances. Figure 6 reveals that the first possibility is the actuality. The median values of the two distributions differ widely (1.15 s and 1.95 s). Furthermore, fully 95% of the data points for the sluggish dances exceed the median value for the lively dances. Thus we see that the sluggish dancers typically took more time between waggle runs than did the lively dancers.

Discussion

Decision-making abilities

The primary goal of this study was to assess the accuracy of decision making by honey bee swarms. Because decision making is a process whereby a course of action is chosen from a number of alternatives, the accuracy of a decision-making process can be evaluated by ranking the alternatives and seeing how well the process chooses the best one. When we presented swarms with a choice among five potential home sites, one excellent and four mediocre, in four out of five trials, the swarm succeeded in choosing the best site for its future dwelling place. Furthermore, we observed that the swarms tended to find all the available nest sites, and that their order of discovery did not determine a swarm’s choice. Our results are consistent with the findings of previous tests of the decision-making abilities of honey bee swarms. When Lindauer (1961) gave a swarm a choice between two equal-sized hives, one sheltered by brush and the other not, he observed that 20–30 scouts visited the protected hive and produced lively dances whereas only 3 scouts visited the exposed hive and they announced their find with sluggish dances. Moreover, when Lindauer transposed the protective covering from one hive to the other, the few bees at the second hive began performing lively dances while those from the first hive ceased dancing. Lindauer's swarm was evidently able to choose the more sheltered nesting site. Likewise, when Seeley (1977) gave a swarm a choice between two nest boxes, a 5-l and a 25-l box, he observed that the swarm reliably chose the larger box when he reversed the volume settings of the two boxes. It should be noted that both Lindauer (1961) and Seeley (1977) gave their swarms a simple decision-making problem, one in which the swarms chose between just two sites which differed greatly in quality. Nevertheless, their swarms did choose correctly. Taking all available evidence into consideration, we conclude that honey bee swarms generally make accurate decisions.

We feel that the results of our five-nest-box experiment demonstrate that honey bee swarms are impressive decision makers, but we must raise one small point of caution in interpreting the results of this experiment. It concerns the way we determined the quality of the two nest-site types that we offered in this experiment: we "asked" the bees. In doing so, we assumed that the type of site that the bees liked most (a 40-l cavity with a 15-cm^2 entrance) is a high-quality site, and that what they accepted when nothing better was available (a 15-l cavity with a 15-cm^2 entrance) is a medium-quality site. Ideally, however, the different nest-site types would be evaluated based on fitness measurements of colonies occupying the different types of site. Such experiments are currently underway, but the results will not be available for several years. In the meantime, our conclusion that swarms are good decision makers rests on the (robust, we think) assumption that the bees' housing preferences are adaptive. Studies of other animals – including birds (Nolte and Fulbright 1996; Regehr et al. 1998), reptiles (Shine et al. 1997; Wilson 1998), insects (Morse 1985; Kaspari and Vargo 1994), and fish (Courtenay and Keenleyside 1983) – certainly have found that the nest-site preferences of animals enhance their reproductive success.

Decision-making mechanisms

We have seen (Fig. 5) that an important part of a swarm's ability to implement the best-of-*N* decision rule is the way that scouts adjust the recruitment rate to a potential home site as a function of its quality. The better the site, the stronger the recruitment, the speedier the buildup of bees, and the likelier the site will be chosen. Video analysis revealed a crucial mechanism underlying the correlation between site quality and recruitment rate: a bee produces more waggle runs per dance if advertising an excellent rather than a mediocre site. Moreover, we found that a bee advertising a superior site produces more waggle runs per dance by producing waggle runs both for a *longer time* and at a *higher rate*. And because a higher rate of waggle-run production creates a dance that appears more lively, our findings support one of Lindauer's (1955) observations in his pioneering study of decision making by swarms: scouts from the best site dance with the most endurance ("ausdauerndsten") and the most liveliness ("lebhaftesten").

One benefit of the bees' tuning their dance behavior to site quality is the way it ensures slow buildup of scouts at sites that are mediocre. As shown in Fig. 5, in each trial except trial 4, the number of bees at each of the medium-quality sites rose more slowly than at the high-quality site. Even in trial 4, the buildup at all the medium-quality sites was slow; one of the medium-quality sites was eventually chosen only because (strangely) there was negligible buildup at the high-quality site. This pattern of slow recruitment to a mediocre site seems highly adaptive. First, it enables a swarm to maintain its connection to a mediocre site, which will be advantageous if this site turns out to be the best available. Because each scout gradually loses enthusiasm for her site and eventually stops visiting it (Seeley and Buhrman 1999), there must be some recruitment to a site for a swarm to stay connected to it. Second, slow recruitment to a mediocre site helps a swarm avoid making a decision too quickly, which will be advantageous if an excellent site is eventually located. In other words, by recruiting only slowly to mediocre sites, the bees give themselves time to continue searching for a better site without losing touch with the moderately desirable sites they have already found. This is precisely what happened in the first three trials of our five-nest-box experiment: the bees first discovered several medium-quality sites and stayed in touch with them for several hours during which time they succeeded in finding the high-quality site. Then, because the bees from the high-quality site danced more strongly that those from the medium-quality sites (see Table 1), the scouts visiting the high-quality site soon outnumbered those visiting the medium-quality ones and, ultimately, the high-quality site was chosen.

The adaptive tuning of waggle dances that we report here is not limited to bees engaged in house hunting. Bees engaged in nectar foraging are likewise known to adjust the duration and the rate of waggle-run production, but in relation to nectar-source profitability rather than nest-site quality (Seeley et al. 2000). Both duration and rate of waggle-run production increase with rising nectar-source-profitability. Moreover, a nectar forager, like a house hunter, adjusts the rate of waggle-run production by adjusting the mean duration of the return-phase portion of her dance circuits. And for both sorts of bees, dances with different levels of liveliness differ in mean durations of the return phase. Perhaps all dancing bees use the same behavioral adjustments to tune their waggle dances to the desirability of their recruitment targets.

One thought-provoking detail of the results from our two-nest-box experiment is that whenever we thoroughly degraded the high-quality nest box (by enlarging its entrance from 15 to 60 cm^2), and so suppressed the dancing for this site, we soon recorded a surge in number of scouts at the medium-quality nest box (see Fig. 4). Notice too in our five-nest-box experiment that whenever we saw a rapid buildup at the chosen site, we registered little or no buildup at the rejected sites (see Fig. 5). These patterns suggest that the groups of bees representing the different nest boxes were able to inhibit each other's recruitment, and that the strength of each group's inhibitory effect was a function of its own recruitment activity. Such cross-inhibition in swarms may enhance their ability to respond differentially to nest sites that differ in quality, just as cross-inhibition in many organisms helps them discriminate between stimulus sources that differ in strength (Young 1989).

What might be the mechanism of cross-inhibition in swarms? One possibility is a "friendly competition" for dance followers. In support of this hypothesis, Visscher and Camazine (1999) present evidence which suggests that when a house-hunting bee chooses a dance to follow, she makes a random choice. Random dance choice was previously demonstrated for bees engaged in nectar foraging (Seeley and Towne 1992), so bees engaged in house hunting plausibly behave likewise. If so, and if the effectiveness per waggle-run of dances for nest sites does not vary (just as it does not vary among dances for nectar sources; Seeley and Towne 1992), then the relative rates of recruitment to different sites should be proportional to the relative numbers of waggle runs produced for the different sites. This could explain the phenomenon of cross-inhibition in recruitment to different sites. In swarm 98-1, for example, between 1045 and 1245 hours, there was dancing for both the 40-l and the 15-l nest box, but much more dancing for the 40-l nest box (see Table 1), and most of the recruitment was to the 40-l nest box (see Fig. 4). But after 1245 hours, when the 40-l nest box was rendered unacceptable and was no longer advertised by dances, the bees dancing for the 15-l nest box had no competition for the attention of the dance followers. This could explain why the number of bees at the 15-l nest box then skyrocketed.

The nearly unbounded rationality of honey bee swarms

Although early students of decision making viewed the minds of humans and other animals as if they possessed supernatural powers of reason, boundless knowledge, and unlimited time to make decisions (Stigler 1961; Raiffa 1968), more recent investigators of decision making have recognized that humans and animals make decisions with limited computational power, knowledge, and time (Simon 1982; Gigerenzer and Todd 1999). Such real-world decision making – called "bounded rationality" – uses approximate methods (heuristics) to solve problems. These heuristics generally involve reducing either the *breadth* or the *depth*, or both, of the decision maker's consideration of the alternatives. For example, one decision-making heuristic called "satisficing" reduces the breadth of the decision-making task. It takes the shortcut of setting an acceptance threshold and ending the search for alternatives as soon as one is encountered that exceeds this threshold (Simon 1956). Another decision-making heuristic called "one-reason decision making" reduces the depth of the decision-making task by basing the decision on just one important property of the alternatives rather than on a complex combination of properties (Gigerenzer and Goldstein 1999). In general, the use of heuristics simplifies the information gathering and processing that is required of the decision maker.

In light of the bounded rationality of real-world decision makers, decision making by honey bee swarms is particularly noteworthy. For although honey bee swarms are boundedly rational – no doubt they lack complete knowledge of the available nesting sites – they do make nest-site selections without greatly reducing either the breadth or the depth of their consideration of the alternatives. A swarm typically makes its decision only after its several hundred scout bees, working together, have examined a dozen or more alternative nesting sites (Lindauer 1955; Seeley and Buhrman 1999) and have assessed each of the alternatives with respect to at least six distinct properties (reviewed in Seeley 1985; Witherell 1985). Thus honey bee swarms pursue an unusually sophisticated strategy of decision making, one that involves nearly all of the information relevant to the problem of choosing the best home site. No doubt it is this thoroughness of information gathering and processing that underlies the success of swarms in implementing the best-of-*N* decision rule. Our next challenge is to understand how hundreds of scout bees work together to produce the high level of information acquisition and processing that is achieved by a swarm as a whole.

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