Collective decisions and cognition in bees

In a remarkable example of collective decision-making, swarms of honeybees, *Apis mellifera*, choose one of many nest sites discovered and reported by their scouts. At first, dancing scouts communicate the location of many sites, but within a few days all dances focus on the same high-quality site[1–3]. Instead of swarms acquiring global information by direct comparison of sites, we find that the swarm's decision arises through a self-organized process driven by the dynamics of interacting individuals following simple rules based on local information4,5.

The number of scouts increases at nest sites through the positive-feedback process of recruitment, and decreases by attrition at less-favoured sites, allowing unanimity to develop[6]. Two hypotheses have been proposed to explain the attrition: scouts either compare sites directly and choose the better one[2], or they drop out of the process after reporting on sites they find[1]. All three scouts observed in one study[1] visited (and perhaps compared) more than one site. If such a comparison really is crucial to the decision-making process of bee swarms, it would indicate that individual bees are capable of complex cognitive processing[7,8].

We tested whether scouts that dance for one site are selective in dance-following. Do they follow dances for their own site (to assess the number of scouts investigating it), for sites they have not visited (such crossover dance-following would be indicative of cognitive ability[7]), or do they follow dances at random? In a desert area where nest sites could be controlled, we observed swarms while they chose between two identical nest boxes[6]. We marked each dancer individually when she first danced, and videotaped all dancing and dance-following by marked bees throughout the decision-making process. The dancing performed for each of the two sites was measured from the discovery of the first nest site to the time the swarm took off. We calculated the distribution of dances available for each marked dancer at times after her first dance, and found that dance-following fits this random expectation (Fig. 1): scouts followed dances for two sites in proportion to the total amount of dancing by others for these sites.

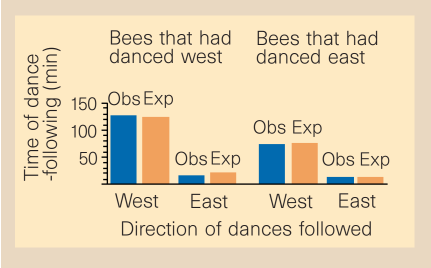

Figure 1 Time for which bees that had danced for the east or west site then followed dances for each site. Obs, observed, and Exp, expected, dancing times. For site S (and for site A), n_S is the number of bees that were marked dancing for site S, F_i is the total time bee *i* spent following dances, D_S and D_A are the number of dances for S and A (excluding those of bee i) during minute *t*, and t_i is the time at which bee *i* first danced. Expected (S) in minutes is given by $\sum_{i=1}^{n_S}\left(F_i \times \sum_{t=t_i}^{\text{takeoff}}(D_S)_t \;/\; \sum_{t=t_i}^{\text{takeoff}}(D_S+D_A)_t\right)$. There is no significant difference between observed and expected values ($\chi^2 = 0.41$, $P = 0.94$).

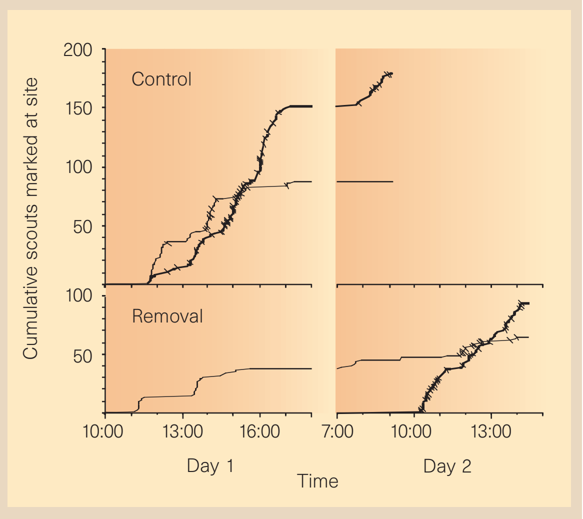

Figure 2 Cumulative number of scout bees marked at south and north sites as the swarm decided between them. South, heavy line; north, fine line. Crossover occurred in both directions (average of 18 ± 10% of scouts; $n = 6$) and was the same for favoured and unfavoured sites, and 'removal' and control treatments (arcsine transform: $t_{10} = 1.50$, $P > 0.19$; $t_4 = 1.06$, $P > 0.38$). All swarms reached unanimity (two controls chose north and one chose south; one 'removal' chose north and two chose south). In each treatment, two swarms moved on the second day after they were set up (as here), and one on the third day. Total scouting time until movement (including only time between first and last dancing each day) did not differ: 13.0 ± 3.3 hours in three 'removal' replicates, and 13.2 ± 1.7 hours in three control replicates ($t = 0.12$, $P > 0.9$).

We then tested the role of direct comparison in the decision-making process. If comparison is prevented, the bees might fail to reach a unanimous decision, or they might take longer to decide. We marked all scouts that inspected each site, and each bee that danced, with coloured paint. In 'removal' replicates, we captured and removed 'crossover' bees that visited a second site; in 'control' replicates, we captured, marked and released crossovers. Preventing bees from making comparisons and dancing for the alternative site did not prevent or delay swarms from arriving at a decision and taking off. The build-up of scouts at each nest box is shown in Fig. 2 for the shortest replicates: the time course of the decision is similar in these, as it is overall.

Direct comparison of potential nest sites by scouts is therefore probably not an important part of the collective decision-making process by swarms. Instead, the decision arises from local information and the properties of the underlying dynamic interactions among individuals, who do not need a global view, which is characteristic of self-organized systems[4,5,9]. Recruitment's positive feedback (probably modulated with respect to site quality,[6] as is recruitment to nectar[10]) and stochastic factors, including individual differences between bees and time of discovery[9], would account for differences in build-up, but not for attrition of scouts from less-favoured sites.

As direct comparison and crossover to favoured sites do not drive attrition, it may be more important that bees drop out of the process after some dancing, leaving the process to succeeding cohorts of scouts[1,6]. This is one way in which recruitment to nest sites differs from that to food sources, as it allows differences in positive feedback between sites to drive the process to unanimity by overwhelming the lower recruitment for less-favoured sites.

Thus the collective decision of a swarm seems to be based not on complex cognitive comparison, but on more limited cognitive tasks and information feedback. Although it is self-organized, this process has been shaped by natural selection on the behavioural components (such as scouts dropping out and recruiters following the dances of others) that determine its workings. Nature can build complexity in this way by using local information and simple rules.

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