Animal behaviour

How self-organization evolves

P. Kirk Visscher

Self-organized systems can evolve by small parameter shifts that produce large changes in outcome. Concepts from mathematical ecology show how the way swarming bees dance helps them achieve unanimous decisions.

Figure 1 **A swarm of honeybees clustered after leaving their natal colony, while searching for a new nest site.**

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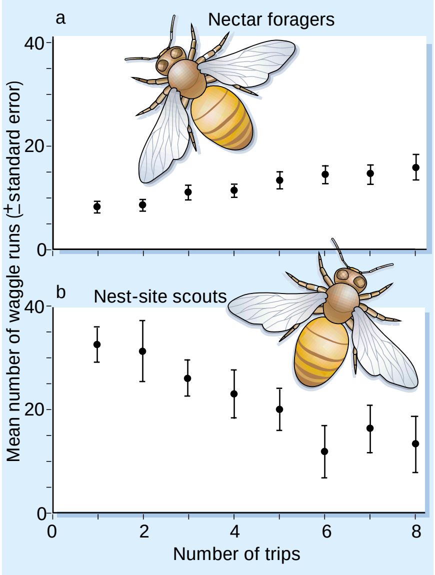

Figure 2 **Different patterns of dance language in nectar foragers and nest-site scouts. These graphs plot the number of waggle runs in the recruitment dances performed after each return trip to the colony for successive instances where each individual bee danced[10].** a, **Nectar foragers continue to dance for many trips. (Here, 93% of 40 foraging bees in 3 colonies danced on more than 8 trips; most danced on more than 50 trips.)** b, **Nest-site scouts, searching for a new home following swarming, perform dances with more waggle runs at first, but soon cease to dance entirely. (Here, fewer than 5% of 86 bees in 3 swarms performed more than 8 dances.) Myerscough's analysis[1] suggests that this difference in dance performance underlies the difference in outcome: in foraging, it is desirable to recruit new foragers for several sites; in swarming, unanimity for a single site must be reached.**

In work published by *Proceedings of the Royal Society*, Mary Myerscough[1] has taken a novel approach to the modelling of group decision-making by honeybee swarms when they are in search of a new home. Bees 'waggle dance' to communicate locations of food in foraging, and of potential nest sites when a colony moves during swarming. Myerscough treats the scout bees dancing for alternative sites as populations, and models their growth and extinction with the tools of mathematical ecology. From this approach it is evident how a slight difference in the way the dance-language 'recruitment' of other bees is structured in foraging and house-hunting influences the outcome of each process.

The choice of a new home site by a swarm of honeybees is a striking example of group decision-making. When a swarm clusters after leaving its natal colony (Fig. 1), scouts search the countryside for cavities with the appropriate volume and other characteristics[2]. They then return to the swarm, and communicate the distance to and direction of the sites they have found with waggle dances[3], just like those used for communicating locations of food sources in foraging[4]. Usually, the scouts find and report several sites, but in time dances cease for all but one of them, and finally the swarm flies to the selected cavity. Self-organizing processes such as this, in which a complex higher higher-order pattern (here, the development of a consensus on the best site) arises from relatively simple responses of individuals with no global view of the situation, are receiving increasing attention as biological mechanisms for elaborating complexity[5].

The population-biology metaphor is appropriate for analysing honeybee dance information. Bees recruited by dances for a particular site may visit it and in turn dance for new recruits, so dances reproduce. But nest-site scouts may cease dancing before they recruit at least one other dancer: the population of dancers for that site then declines, and may become extinct. Myerscough's approach incorporates key aspects of the dynamics of nest-site recruitment, and can accommodate differences that are specific to the nest site or the individual bee. The populations of dancers have 'age structure' in the sense that some dances are a scout's first dance for a nest site, others follow a second trip, and so on. This is similar to population growth with discrete generations, which can be represented in a standard tool of mathematical ecology: a Leslie matrix. The 'age structure' patterns also can incorporate an important difference in dance language use between nectar foraging and house-hunting. In foraging, the number of waggle runs that a bee performs when returning with food increases and then levels off with successive dances by that bee (Fig. 2a). In contrast, in house-hunting, the number of waggle runs (which initially depends on the quality of the site) generally declines with each successive dance (Fig. 2b), and each scout soon ceases dancing entirely. This gives different patterns of 'age-specific fecundity' to the dancing bee populations.

Because the mathematical theory of models of this type is well developed, Myerscough's approach has an analytical payoff. It is straightforward to predict whether a population of dancers for a site will increase or decline. However, this is a dynamic process, because only a limited number of scouts can be recruited. As a result, whether dancers for a particular site increase or decrease in number depends both on the quality of the site and on the populations of other dancers. The dancing for a site may increase while competing dances are rare, but then decline in favour of other sites with greater 'fecundity' (that is, those that elicit a greater number of waggle runs of dancing per trip by scouts). Such dynamics are typical of swarms[3,6,7], with the outcome that the highest-quality site among those discovered is usually selected[8].

The most striking result of this approach is that it shows how certain special features of the dance in the context of house-hunting ensure that one, and usually only one, of the populations of nest-site dancer ends up with all available recruits. This finding is of wide interest, because it shows how natural selection can shape a self-organizing process. In both foraging and nest-site scouting, global patterns of allocation of bees among alternative resources arise from interactions of bees responding to their own experience, without a global view of the pattern of allocation or direct knowledge of the characteristics of alternative sources[9]. However, the contexts of nectar foraging and nest-site decision-making differ in one key respect. In foraging it is usually desirable for the bee colony to use several food sources simultaneously, especially if they are similar in quality; in house-hunting the colony has to settle on just one of multiple sites, even if they differ little in quality. The dance language is used to recruit bees in both settings, but certain aspects of how the dance is performed are different. Myerscough shows it is just these parameters that determine the outcome. Attrition in dances in the Leslie matrix models mathematically ensures that one resource will always dominate in nest-site selection (unless stochastic differences intervene, which may account for the occasional failure of swarms to achieve unanimity). But in foraging there is no advantage to doing this, and attrition does not occur.

A common misconception about self-organization in biological systems is that it represents an alternative to natural selection[5]. This example illustrates how natural selection presumably evolves such mechanisms: slight modifications of key components shape the parameters of the self-organizing system, and shift the ensuing large-scale patterns to achieve different ends. ■

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