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Social Learning: The Importance of Copying Others

A new study argues that social learning is adaptive because ‘demonstrators’ inadvertently filter information, so that copiers learn behaviours that have proved successful. There are remarkable parallels between these findings and data on how social insects share information about food locations.

**Christoph Grüter,
Ellouise Leadbeater,
and Francis L.W. Ratnieks**

In humans, learning by observing or asking others can save time and effort. For example, a traveller can bypass the need to check out the numerous available restaurants in an unknown city by asking the residents where there is a good place to eat. However, relying on others can be a risky strategy. The person you rely on might have a different taste, a bad memory, or not have visited a restaurant for years. An inability to avoid out-of-date or unreliable information is considered a major pitfall of social learning. As a consequence, theory has predicted that both individuals and populations should usually employ a mixture of both social and individual learning [1–4]. A new study by Rendell *et al.* [5] challenges this view and argues that social learning is usually superior.

Inspired by a classic evolutionary tournament [6] that investigated the evolution of cooperation, Rendell *et al.* [5] organised a computer tournament in which social learning strategies,

submitted by entrants, competed in a game of natural selection for a 10,000 Euro prize. Each strategy specified when an individual should copy another, when it should gather its own information, and when it should simply use the information it had already acquired. Rendell *et al.* [5] found that the strategies that performed best relied almost exclusively on social learning. Because ‘demonstrators’ have information about the expected pay-off of different behaviours, they selectively perform those that are most beneficial for themselves. By doing so, they inadvertently filter information for all other individuals in the population. As a result, individuals relying mostly on copying acquire high-payoff behaviours as well.

Non-human animals also learn from one another, and one of the most widely-studied examples of social information use pertains, surprisingly, to insects. Honeybees deliberately tell their nestmates where to find food *via* symbolic ‘waggle dances’ [7,8] (Figure 1). In keeping with the authors’ predictions, bees do not dance every time that they find food, but only when the food source is highly profitable [8].

This can be seen as an analogue of the information filtering emphasised by Rendell *et al.* [5]. Indeed, the parallels between the real situation, where bees choose to ‘observe’ (socially learn the location via the dance), ‘innovate’ (individually learn a foraging location by trial-and-error) or ‘exploit’ (rely on spatial memories acquired during previous trips to a known location), and that modelled in the tournament, are clear-cut (Figure 2). Bees provide an opportunity to test these new hypotheses in an ecologically realistic setting [9]. We return to this point later.

The tournament led to other unexpected findings. Successful strategies spent most time relying on the behaviours that were already in the behavioural repertoire, rather than learning new behaviours. In other words, successful ‘individuals’ mostly relied on memory. However, relying on memory is less useful when the environment changes, and correspondingly, increasing the time spent ‘observing’ when the pay-offs of current behaviours dropped was important. Our restaurant visitor, if he followed this strategy, might return to the same restaurant as long as the quality of the food remains acceptable. This avoids the difficulty of finding a better place. But if the prices go up or the food gets worse, then he might do better to ask around for alternatives. Again, the social insects provide a real-world empirical example. Wood ants (*Formica rufa*) and honeybees both cease learning food location

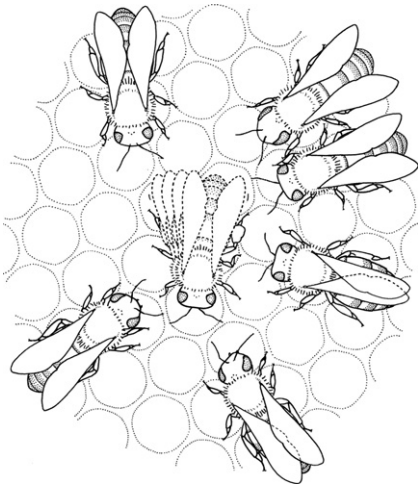


Figure 1. A honey bee pollen forager performing a waggle dance to dance follower bees.

The waggle run (shown) communicates the direction and distance of the flower patch being used by the forager [7,8]. The manoeuvre also provides other types of information such as the food odour which helps foragers to locate food sources [8,12]. Dancing incorporates information filtering: honeybees dance only for high-quality resources and the better the food source, the more waggle runs they perform (longer dances). The number of recruits to a particular food source is proportional to the number of waggle runs [19]. Honey bees use the waggle dance to communicate the location of nectar, pollen, water and resin (propolis), and also nest sites during swarming. Drawing by Lila Morris from video of dancing bee. To see the video go to <http://www.sussex.ac.uk/lasi/resources/education/whatbeesdo>.

socially once they have learned the locations of good renewable food sources [10–12]. As long as their food source remains reasonably profitable, the worker will rely on memories and return to the same place again and again [10]. But if the profitability deteriorates sufficiently the foragers start seeking social information again. Honeybee foragers start paying more attention to waggle dances when foraging at familiar locations becomes unsuccessful as a result of environmental changes [13,14].

Two key factors that affect the value of social learning are the costs of acquiring information and information reliability [1–4]. In the tournament, costs were either equal for social and asocial learning (first stage) or lower for social learning (second stage). Because social learning was already strongly favoured during the first stage, lowering the costs had no major effect.

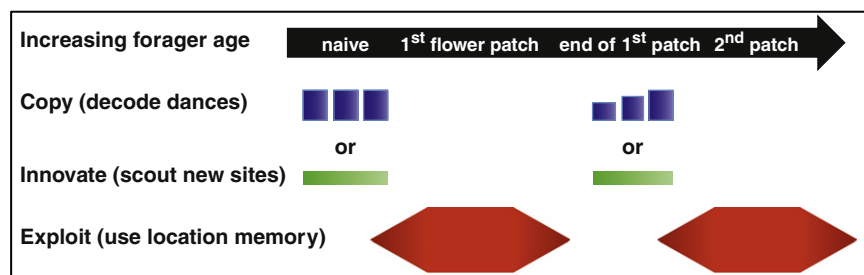
It would be interesting to test a situation where costs for social learning are higher. For example, one might have to walk a long distance to a tourist office to find out about the location of a restaurant or pay for the advice. In honeybees, this situation may be common, because a forager might have to walk around in the nest or wait until she finds a dancing nest-mate [15], which can favour individual exploration and trial-and-error learning [15,16]. On the other hand, bees that learn about food locations by following waggle dances tend to locate better quality flower patches [17]. In other words, social learning can be favoured even if it is more costly. This would explain why more bees find their first patch by following dances than by individual exploration [17].

Another surprising result reported by Rendell *et al.* [5] is that the degree of error associated with social learning had almost no effect on the success of strategies that relied mostly on social versus asocial learning. It is often assumed that unreliability is an important disadvantage of social information [1–4]. In fact, the results suggest that errors might even be advantageous if they lead to the acquisition of novel behaviours and therefore behavioural diversity [5].

The tournament revealed the parasitic nature of social learning strategies in the simulated environment. Strategies that mostly use ‘observe’ are likely to decrease the average fitness of the population because they reduce the behavioural diversity in the population. This is an important difference between the simulated environment with competing

‘individuals’ and social insect colonies, where the fitness of a worker strongly depends on the overall productivity of the colony [18]. In an insect colony, the frequency of social learning versus asocial learning will maximise the foraging success of the colony and not the individual. Therefore, social insects provide an opportunity to investigate altruistic learning strategies: workers that sacrifice energetic benefits in order to obtain information (‘innovate’) that can be provided to other colony members. Some honeybee foragers, for example, do not follow dances but scout for new food patches [19]. Even if such a bee had a low chance of success, it can be highly beneficial for the colony because a newly discovered field of flowers can potentially be exploited by hundreds of nestmate foragers [20].

One of Rendell *et al.*’s [5] aims was to provide a basis for studying the evolution of culture, and in this respect honeybees are clearly poor models. ‘Innovation’ in honeybees does not involve completely new behaviours; rather, they exchange and use stereotyped information about specific features of important resources [9,12,19]. Furthermore, waggle-dance information (and most other social information in social insects) is limited to nestmates and does not propagate widely into the population. Evidence for culture outside human societies is as yet limited, and for the vast majority of group-living animals the more general question of when social information use is adaptive is more relevant than when culture will evolve. Rendell *et al.*’s [5] tournament provides a new tool for understanding when animals should



Current Biology

Figure 2. Diagram showing the parallels between the tournament predictions and how honey bees appear to use information about food sites.

Most naive foragers follow several waggle dances to locate their first food patch (‘observe’). Some search for a new patch without vector information provided by dancers (‘innovate’). Once a patch of acceptable quality has been discovered, foragers rely on their memory to revisit this patch (‘exploit’). When the food patch deteriorates foragers enter a new cycle of ‘observing’ or ‘innovating’.

learn socially, and honeybees provide a ripe resource for testing these hypotheses in an ecologically realistic environment.

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