

Insights from insects about adaptive social information use

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Copying others can greatly improve individual fitness and is fundamental for the organisation of societies. Yet in some situations it is better to ignore social information and either explore the world individually or use personal information obtained through prior experience. Insects provide excellent models to study the strategic use of social information, but insights from recent research have rarely been viewed in the light of social learning strategies. Here we discuss how insects tailor their reliance on social information to those circumstances for which it is most beneficial, and suggest that insects and vertebrates use similar information-use strategies. We highlight future research avenues, including the use of molecular tools to study the genetic and genomic basis of social information use.

Selective use of social information

Animals are often faced with different types of information about their environment, and choosing the type that leads to the most successful behaviour is important but not straightforward [1-6]. Picture a woodland in which an ant forager is searching for honeydew sources. The ant can locate food in different ways: she can follow pheromone trails to new food sources discovered by others, look for new foraging sites herself, or choose to revisit food sources that she already knows about. In other words, she can acquire new information socially, acquire new information by individual exploration, or fall back on the personal information she has obtained, either individually or socially, through previous experience (cf. 'observe', 'innovate', and 'exploit' in [4]). Ants that rely on personal information will find an acceptable food site quickly because they already know its location, and trail followers might also be quicker than explorers. Yet if no ants explore, any new honeydew sources that arise are likely to go undiscovered while existing ones become depleted. Thus, despite potential time, energy, and predation risk costs, exploration could

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0169-5347/\$ - see front matter

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improve individual and colony success when the environment changes.

Decisions like these are repeated throughout the animal kingdom whenever animals face a choice of whether or not to use social information. Social information might be 'cheap' to obtain, because individuals can bypass the costs and risks of exploration [3–5,7–11], and its quality is often assured because other animals tend to display the most profitable behaviours they know of [4,12]. However, the benefits of both social and personal information (trailfollowing or revisiting in our ant example) depend critically on the likelihood that resources change and on the behaviour of other individuals [4,7,13]. Clearly, animals should choose the option that will lead to the greatest payoffs in the context in which they find themselves, but how can they assess these potential payoffs in a complex and changing environment?

Here we discuss why insects provide tractable and varied model systems to study the adaptive use of social information in different contexts. We see that insect worlds involve both social environments and forms of social information that are rare or non-existent elsewhere and offer vast potential for experimental manipulation. For instance, in the social insects, social information use has

Glossary

Eusocial society: animal society characterised by reproductive division of labour between reproductive and (partially) sterile individuals. Brood care is cooperative and adult generations overlap (so adult workers might care for broods that are their siblings).

Exploration: gaining new information about the environment through individual sampling.

Personal information: information about the environment (e.g., the location of a feeding site) that an animal has acquired (either socially or asocially) and acted on previously.

Signal: trait such as a behaviour, or the products of a behaviour, that has been shaped by selection specifically because it conveys information from one animal to another. In the context of this article, we discuss signals that convey information about the environment, rather than about the motivation or qualities of the signaller.

(Coincidental) Social cue: trait such as a behaviour, or its products, that conveys information from one individual to another but has not evolved specifically for that function, such as the presence of an animal at a particular food site.

Social information: information about the environment that an animal acquires through observation or interaction with another animal or its products.

Social learning: learning about the environment that is influenced by interaction with, or observation of, another animal or its products. In the examples discussed in this review, social information use usually involves social learning. However, there are cases in which responding to social information might not necessarily involve learning, such as responses to alarm pheromones.

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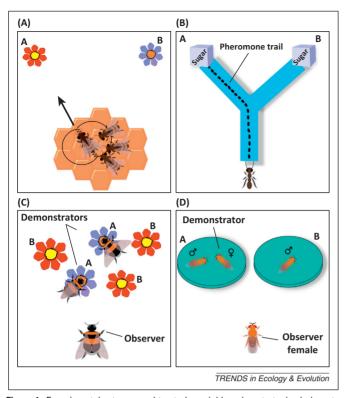


Figure 1. Experimental set-ups used to study social learning strategies in insects. (A) Honeybees [46,56], (B) ants [53,79], (C) bumblebees [68,80,81], and (D) fruit flies [18]. Insects face a choice between two options, A and B. Focal animals (observers) have social information about A and either personal information or no prior information about B. The characteristics of social, personal, and asocial information can be manipulated, for example by increasing the distances of A and B, varying the amount of experience of observers and demonstrators, and manipulating the time interval between exposure to information and testing of the observer. (A) Waggle dancing bee advertising food source A and is surrounded by three observer bees. (B) Forager ant entering a Y-maze that is marked by a pheromone trail leading to food source A. (C) Bumblebee observing bumblebee dummies on one of two flower types. (D) Fruit fly choosing one of two males, one of which is being chosen by a demonstrator female.



Figure 2. A honeybee pollen-forager performing a waggle dance and observer bees. She 'waggles' her abdomen as she walks in a straight line (waggle run), then turns to the left or right to walk back to the starting point (return phase). The better the food source, the more often she repeats the waggle run. The duration of the waggle run provides surrounding bees with information about the distance to the food source. The direction of the waggle run in relation to gravity provides information about the direction of the food source in relation to the sun [22]. The more waggle runs an observer bee follows, the better is her information about the location [90]. Dance followers learn not only of the food source but also its odour [91]. (Photo by C. Grüter.)

Box 1. Social learning in insects

In 1973, Karl von Frisch won the Nobel Prize for discovering that honeybees can communicate the location of a profitable resource by means of the waggle dance (see Figure 2 in the main text), but he and other authors before him built on a wealth of evidence that insects use social information. For example, by the time he discovered the 'dance language', he had already demonstrated that honeybees use the presence of other bees on flowers to identify food sources (local enhancement) and that bees learn food odours inside the nest while following dances and receiving food samples from foragers (social enhancement of food preferences) [22]. Both types of social learning have since been found in many other social insects: the scent and flavour of food collected by returning foragers and learned inside the nest guide foragers to rewarding flowers in bumblebees [82], stingless bees, wasps [17], and ants [83].

In the field, the foraging choices of many pollinators are further refined according to the presence of other foragers (wasps [84], bumblebees [80], stingless bees [17]) and chemical cues left by other foragers either inadvertently [17] or as evolved pheromone trails [16,17]. In some ant species, foragers actively guide nestmates to food sources or nest sites, a behaviour known as tandem running (http://www.youtube.com/watch?v=Kam0jKiAk3c) [16,48,85]. In several instances it has been shown that social insects use social cues or signals produced by heterospecifics, rather than their own species, to find food [17,69]. Most examples of social learning have been studied in the context of foraging, but bees, ants, and wasps also rely heavily on social information when hunting for new nest sites and during colony defence [86,87].

Although the historical focus has been on eusocial species, more recent studies show that social learning guides important decisions in non-colonial insects and other invertebrates too [18–21,88,89]. Crickets and damselfly larvae use social cues to avoid predators [23,89] and it has recently been shown that the fruit fly *Drosophila melanogaster* uses social information in a variety of contexts [18–21], such as when choosing oviposition substrates or mates (see Figure 1D in the main text).

often evolved into signalling, and these signals can easily be monitored, changed, or removed altogether. Moreover, it is possible to simulate ecology in the laboratory in a realistic manner while varying the costs and benefits of the different options (Figure 1). Insect social systems also incorporate variation in relatedness, providing the raw material to investigate the evolution of 'parasitic' social information-use strategies. Finally, insects provide genomically tractable models with short generation times to capitalise on the enormous potential offered by rapidly developing molecular technologies [14,15].

Social information use in insects is widespread and diverse (Box 1) [16,17]. Although non-colonial insects such as the fruit fly *Drosophila melanogaster* have recently been established as potentially powerful social learning models [18-21], the greatest research effort has focused on the eusocial Hymenoptera [22,23], and the discovery of the honeybee waggle dance (Figure 2) is widely recognised as one of the most important developments in the study of animal behaviour (Box 1). Eusociality involves frequent social interaction and overlapping generations, favouring the evolution of social learning [24–26]. Individuals share mutual interests in colony success, so 'demonstrators' benefit from providing social information and coincidentally informative social cues have thus repeatedly evolved into signals through ritualisation and amplification [16,27]. Yet for this very reason, social insects are not traditionally discussed in the social learning literature, because responding to evolved signals rather than coincidental social cues

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