

Dispatches

Social Learning: Public Information in Insects

Although it has received less coverage than in vertebrates, the study of insect social learning has a rich history with spectacular examples of how individuals extract knowledge from other animals. Several new studies on crickets and social bees have now shown how insects can adjust their behaviour adaptively by making use of cues generated inadvertently by other individuals.

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The rapid expansion of the field of social learning in recent decades [1,2] has almost entirely bypassed the insects. Yet, a close inspection of the literature reveals numerous cases where insects appear to learn by observation, eavesdrop on members of the same or different species, and even engage in teaching other members of a society. In fact, the first hint of observatory learning by animals dates back to Darwin's field notes published by Romanes [3,4]. Darwin suggested that honeybees learn the art of nectar robbing — extracting nectar from flowers via holes bitten into the tubes, without touching the flower's reproductive organs — by observing bumblebees engaged in the activity. Experimental proof for this conjecture remains outstanding, but it is interesting to note that Darwin thought that observatory learning might occur across, rather than within, species (Figure 1). This deserves more consideration, and we will return to it later.

Early in the 20th century, researchers became aware that many adult phytophagous insects prefer host species that they themselves had fed on when they were larvae — even where the insect species, as a whole, was a generalist with multiple acceptable hosts [5]. In what has become known as Hopkins' host selection principle, it was thought that the larvae become conditioned to the chemosensory cues associated with food provided by their parents [6]. This is a non-trivial suggestion, as the nervous system of a

holometabolous insect is extensively rearranged and rewired during metamorphosis [7]; nevertheless, there have been convincing studies to show that such pre-imaginal conditioning indeed occurs [8]. This shows that insect parents can pass on valuable information about suitable food types to their offspring, simply by placing eggs on suitable host plants, or by provisioning eggs with certain food types [9]. In a similar vein, Kirchner and Lindauer [10] considered the possibility of 'traditions' being established in honeybees colonies. Foragers can be trained to feed at a certain time of day, and it was shown that these learnt temporal preferences are picked up by larvae via vibratory cues. The individuals so taught will display the same preferences when they themselves become foragers.

One of the most spectacular examples of social learning occurs in the honeybee dances. Inside the darkness of the hive, successful foragers display a series of stereotypical motor behaviours which inform other foragers of the precise location of floral food, up to several kilometres away from the hive [11]. Dancers essentially 'teach' recruits by putting them through a symbolised version of the 'real life' flight to the food source. Recruits memorise and decode the information delivered in the dances, and subsequently apply on the flight to the indicated food source [11]. Note that this constitutes a form of observatory (unrewarded) learning: while dancers occasionally give food samples to recruits by regurgitating food [11], these food

samples are not a prerequisite for successful information transmission (T. Seeley, personal communication). Such mouth-to-mouth contacts between bees, however, serve another function in the context of social learning: successful foragers can teach their nestmates the scent of the food they have located [12].

With the exception of Darwin's suggestion that honeybees might copy bad habits from bumblebees, the examples above are all cases where the transmission of information is of mutual interest, for example between parents and offspring, or between members of a colony of related individuals. A recent focus in social influences on learning, however, concerns cases where individuals inadvertently leave cues that can be used as publicly available information by other individuals for adaptive behaviour [2]. A relatively simple form is local enhancement, where animals are drawn to sites where conspecifics are present [1]. The newcomers may then learn, on their own, that the site contains valuable food, for example in Vespidae wasps [13]. Bumblebees are attracted to members of the same species when they scout for a novel flower species [14], and can learn about suitable food sources by

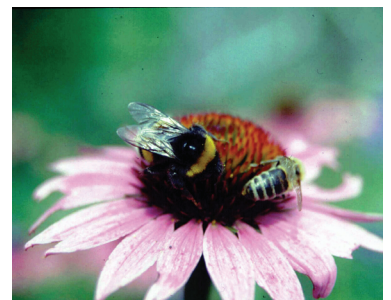


Figure 1. Learning from other species? Darwin suggested that honeybees might learn from bumblebees not just which flowers to visit, but also might imitate the particular motor patterns to best extract the nectar, via observatory learning. (Photo by J. Spaethe.)



Figure 2. A lonely cricket in trouble.

In this issue, Coolen *et al.* [17] report that this cricket could well have avoided its impending death — if only it had observed how conspecifics respond to predation threat. (Photo by O. Dangles.)

observatory learning from unrelated individuals, without the necessity of direct interaction with these individuals, and without the presence of rewards [15]. This means that bees, by observing the activities of other foragers, can bypass the substantial costs of exploring multiple food sources by individual initiative [16].

In this issue of *Current Biology*, Isabelle Coolen and co-workers [17] report for the first time that insects can use public information to learn about danger, too (Figure 2). In an elegant set of experiments, Coolen *et al.* [17] made use of the hiding response that juvenile wood crickets show in the presence of a natural predator, the wolf spider. Observer crickets were placed in leaf-filled boxes accompanied by conspecifics that had either recently experienced a high spider predation threat, and were accordingly tending to hide under the leaves, or that had had no recent interactions with predators. After 6 hours, observers whose companions had been exposed to the dangerous environment were themselves more likely to be found hiding than those whose companions had no recent spider experience. As the observer crickets had no direct interaction with spiders themselves, nor with any material which had been in contact with them, this hiding

behaviour could only have been elicited through their 'fearful' conspecifics. The most novel aspect of this study, however, occurred when the authors then removed all demonstrator crickets from the boxes, and found that these behavioural differences could still be observed even 24 hours later. Rather than simply hiding when others were hiding, the observer crickets continued to be careful even after their 'knowledgeable' companions had been taken away, suggesting that they had learnt indirectly about the danger level in their surroundings.

If crickets usually take a long time to emerge from hiding, these findings could be explained without invoking social learning. But when Coolen *et al.* [17] simulated a stressful, but not predatory, event in a control experiment, crickets re-emerged within 45 min. Furthermore, observer crickets did not show increased hiding behaviour when separated from demonstrators by a partition allowing pheromone exchange but no visual contact, or when placed in boxes that had previously contained crickets in danger from spiders. Intriguingly, rather than simply inducing a hiding response, the behaviour of the fearful demonstrator crickets must have provided their naïve companions with an indirect

assessment of a local predation threat — information which may undoubtedly be costly to ignore.

That the first clear demonstration of the use of public information about danger in insects was made with a non-colonial species that is not associated with complex social bonds serves only to emphasise, as Coolen *et al.* [17] point out, that learning from others can be adaptive even when individuals are unrelated, and as Darwin suggested, potentially even when they belong to different species. The possibility that animals can obtain useful information from the behaviour of other species is little considered (but see [18,19]).

Information about water and food availability, food toxicity, predator threats, etc. will often be of relevance for more than one species, and animals would do well to use public information from members of other species. Humans, for example, will certainly have benefited from such observations in evolutionary time. In the 1974 film *Animals are beautiful people*, for example, Kalahari tribesmen use clever techniques to extract from baboons the information about hidden access to water reserves — essentially by overfeeding the baboons with salt, then following them after release as they rush to the water. Turning to insects, *Trigona* stingless bees engage in espionage of the scent trails of other bee species to a rich food source, and subsequently take over that food source by driving away or even killing their competitors [20]. It remains to be determined whether this behaviour is learnt, or a form of inter-specific local enhancement.

One of the authors of this dispatch, in his preschool years, attempted to levitate by flapping his arms after observing ducks in the park, and to increase his running speed by imitating the sound of a galloping horse. Neither of these produced satisfactory results, indicating to this author that birds and equines were not suitable role models for locomotion. But the suggestion here is this: some animals might be relatively flexible in what other

animals they copy, and subsequently evaluate the usefulness of the copied behaviour, or the usefulness of the particular model in general. The study of heterospecific information transfer could thus be a useful avenue of future research, in both insects and the less successful other animals that populate the planet.

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Cytokinesis: Rho Marks the Spot

During cytokinesis of a eukaryotic cell, following the chromosome movements of anaphase, a contractile ring forms in the cortex midway between the segregating chromosomes and divides the cell into two daughters. Recent studies have provided new insights into the mechanism by which the site of contractile ring assembly is specified.

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When a eukaryotic cell divides, within minutes of anaphase chromosome motion the cortical cytoplasm begins to ingress at a location overlying the position previously occupied by the chromosomes at metaphase. The remarkable ability of cells to specify the site of contractile ring formation so precisely has fascinated and frustrated biologists for decades. New work [1–3] has now shown that active RhoA forms a narrow zone at the site where the contractile ring will form, and identified the Rho GTPase-activating protein (RhoGAP) component of the centralspindlin complex and the GTP exchange factor for RhoA as key players in the activation of RhoA.

Microtubules Specify the Site of Contractile Ring Formation

It has long been recognized that some component(s) of the mitotic spindle plays a key role in determining the site of cleavage furrow formation when a eukaryotic cell divides. Support for the idea that the spindle delivers a signal to the cortex has come from experiments in which the spindle was repeatedly repositioned in an artificially elongated embryonic echinoderm cell [4]. The results showed that multiple furrows can be sequentially specified, demonstrating that the cortex of the anaphase cell is globally competent to furrow, provided that the appropriate signal is delivered and received. Micromanipulation experiments, also performed in echinoderm

blastomeres, showed that two astral arrays of microtubules, lacking intervening chromosomes, are sufficient to generate the signal for furrowing [4].

Subsequent work in mammalian and *Drosophila* cells, in which the geometry of spindle, asters and cortex differs from that in large, spherical embryonic cells, suggested that interzonal, not astral, microtubules are required for cytokinesis [5]. Given these conflicting results, much effort has been focused on determining which class, or classes, of microtubules are responsible for furrow induction. It is now generally agreed that microtubules are the only structural component needed for furrow induction [6], and that the class, or classes, of microtubules that are required depends on cell type. In some cases, two sequential signals from astral and interzonal microtubules are used [5,7]. The finding that different arrangements of microtubules contribute to specification of furrowing in different organisms and that multiple signals may participate