

Encyclopedia of Animal Behavior (Ed by M. Breed and J. Moore). Elsevier.

Social learning in insects

Reuven Dukas

Animal Behaviour Group, Department of Psychology, Neuroscience & Behaviour,
McMaster University, 1280 Main Street West, Hamilton, Ontario, L8S 4K1,
Canada

Key words: ants, bees, communication, flowers, fruit flies, insects, social behavior, waggle dance.

Introduction

Our understanding of insect learning has changed dramatically in the past few decades and only recently has it become well established that learning affects all major insect activities including feeding, predator avoidance, social interactions and sexual behavior. Whereas we understand individual learning in insects rather well, the role of social learning in this diverse group is still not clear. Until recently, there have been no research programs devoted to examining insect social learning. Furthermore, students of insect behaviour who worked on topics relevant to social learning typically did not relate their research to the literature on social learning, which has focused on vertebrates. Examples provided below include studies on intergenerational transfer of substrate preference in a variety of insects and communication about food in eusocial insects.

My brief review of insect social learning begins with general considerations of how the characteristics of insects could affect the prevalence of social learning in this large and diverse group. I then divide my analysis of what is known about socially influenced learning into two parts, one devoted to the majority of insects that are solitary, and the other to the well studied minority that are highly social.

Insect life history and social learning

Social learning has a fitness advantage relative to individual learning only under a restricted set of conditions (See Laland, this volume). Such conditions may not be widespread among insects, suggesting that social learning may occur only in a small proportion of insect taxa. Below I discuss two key life history traits that may limit insects' use of social learning.

Lack of parental care

Social learning is perhaps most beneficial for young, inexperienced individuals while they are being cared for by their more experienced parents. The life history of many vertebrate species requires a period of parental care, during which dependent young can acquire reliable information from their parents. For example, most song bird (oscines) males must hear their fathers sing when young in order to sing properly when sexually mature, and, in some species, young of both sexes imprint sexually on their opposite-sex parent. Vertebrate-like

parental care, however, is rare in insects. Even in the exceptional cases where an insect cares for her young, for example, in some sand wasps (tribe Bembicini), parental care is limited to the adult providing food for her larvae inside the underground burrow. Because parents and offspring do not spend time together above ground in the settings most relevant to adult behaviour, the range of information that can be socially transmitted from parent to young is restricted. Furthermore, little information may survive metamorphosis from larva to adult.

Social interactions between siblings occurs in some insect species. However, siblings typically do not have as great a difference in experience from one another as do parents and offspring. Hence learning from a sibling may not be as beneficial as learning from a parent. Nevertheless, social learning among siblings is known among social insects and is discussed below.

Non overlapping generations

As previously mentioned, social learning is most beneficial when inexperienced individuals can gain reliable information from more experienced ones. In animals with overlapping generations, distinct age groups that differ in their levels of experience typically interact. Consequently, members of younger, inexperienced generations can acquire information from older, more experienced individuals. Many insects, however, have non-overlapping generations. For example, many solitary bees emerge in the spring, provision their nests and lay eggs. The bees usually live for only a few weeks and their offspring do not emerge until the following spring. Such absence of overlapping generations differing in experience in many insects could limit the occurrence of social learning.

Social learning in solitary insects

Social learning is more likely to occur when there are frequent interactions among individuals with a potential to gain from sharing valuable information, as is clearly the case among social insects, which typically share a nest with numerous closely related conspecifics. Because social insects are unique among animals and more likely to possess social learning than solitary insects, they will be discussed separately. Here I address the limited knowledge that we have about social learning in solitary insects, dividing the discussion between insects that interact little with other individuals and insects that typically occur in aggregations.

Truly solitary insects

In many insects, interactions among individuals are limited to courtship and mating. In other circumstances, there may be little contact between individuals that could permit information transfer. Currently, no social learning in the context of sexual behavior is known in solitary insects. Similarly, whereas a variety of insects are territorial and many meet incidentally at food sites, no social learning at feeding sites has yet been described in solitary insects.

Perhaps the best opportunity for social learning to occur among solitary insects involves indirect interactions between mothers and offspring. Many insect species specialize on a single food and possess a species-characteristic

repertoire of behaviors and physiology linked to exploiting that food. In insects that are not extreme specialists, offspring could acquire indirect information about appropriate foods from their mother.

In many insects, the mother either lays her eggs on a food substrate or delivers food to the nest, where she lays her eggs. Although the larvae typically do not interact with their mother, they do consume the food that she has chosen. If larvae succeed in maturing into adults, newly eclosed adults who recognize their mothers' food choice possess reliable, socially acquired information that this food is adequate.

How can newly eclosed adults know what they have eaten as larvae? There are three scenarios, all apparently occur among insects. First, the larvae can simply learn the characteristics of a food that they consume. Individual learning has been well studied in several insect larvae, most notably fruit flies (*Drosophila melanogaster*). The larval memory, however, would have to survive the massive cellular reorganization that accompanies metamorphosis. Neurobiological work in fruit flies indicates that parts of the mushroom body, the brain part involved in olfactory learning and memory, remains intact throughout metamorphosis, suggesting that memory transfer from larvae to adults is mechanistically feasible. However, results of empirical studies of sustained memory through metamorphosis are somewhat inconclusive.

The first careful test documenting survival of memory from larvae to adults in fruit flies involved associating one odor with electric shock and another odor with safety. The fly larvae exhibited avoidance learning of the odor associated with shock and the same individuals tested as adult flies exhibited similar odor-specific avoidance. Whereas attempts to replicate this finding have failed, studies in other insect taxa including moths and parasitoid wasps also suggest that specific memories can be transferred from larvae to adults. These studies await replication.

The other two mechanisms allowing for social transmission of information from larvae to adults do not require survival of memory through metamorphosis. In some insects, the pupal case may contain odors of larval food, which newly eclosed adults can then learn. Finally, various insect species pupate either on the larval food substrate or close to it, so young adults can learn about their larval food upon emergence. Indeed, a few studies in *D. melanogaster* indicate that adults prefer either odors of food remaining on their pupal case or the food substrate upon which they eclose.

Regardless of the mechanism involved, it is clear that intergenerational transfer of information can take place in a variety of insects. Although such information transmission depends upon a simple form of social learning, it can have dramatic ecological and evolutionary implications because such simple social learning can alter patterns of host-plant use by herbivores. Host shift by herbivores can lead to a coevolutionary process of herbivore adaptations to feeding on certain plant species and plant strategies for reducing such herbivory. Furthermore, if herbivores find mates on their host plants, a shift in host plant promoted by social learning could lead to reproductive isolation leading to speciation.

Insect aggregations

Many solitary insects live in aggregations, which vary greatly in the frequency of interactions among aggregation members. Some aggregations are formed because individuals tend to stay where they were born. Other aggregations result from some desirable feature of the substrate, which independently attracts many individuals. Members of neither type of aggregation seem to engage in much social interaction. For example, many solitary bees and wasps nest in aggregations where each female appears to have minimal contact with her neighbors. No social learning among adults is known in these species.

Yet other aggregations are created as a result of active recruitment and attraction of conspecifics responding to species-specific aggregation pheromones. Examples include many fruit flies (*Drosophila spp*), bark beetles (most species of *Dendroctonus* and *Ips*), and locusts (e.g. *Schistocerca gregaria*). To date, no study has documented social learning in actively aggregating species. However, such taxa would be prime candidates for relying on socially acquired information given the frequent social interactions among conspecifics.

Social learning in social insects

Until recently, research on social-insect behavior was disassociated from the literature on vertebrate social learning. Consequently, cases of probable social learning in social insects were typically described as communication, and no critical tests for social learning were conducted. Nevertheless, some well-studied behaviors of social insects clearly involve social learning.

Learning about distant food

Some social insects forage on plentiful, but ephemeral, food sources. For example, a patch of flowers can provide nectar and pollen for many bees, but may cease blooming within a couple weeks. Locating new flower patches is a difficult task. Consequently, bees could benefit from informing their hive mates, typically close relatives, about a rich food source that they have discovered. Indeed, many social bees, wasps and ants (hymenoptera) possess means of communication about distant food sources.

The most celebrated case of such social transfer of information about food is the waggle dance of honeybees (*Apis mellifera*). Foragers (models) returning with nectar from a rich patch of flowers regurgitate their stomach contents to workers in the hive. If a forager senses high demand for her nectar, she performs the waggle dance on the vertical comb inside the dark nest cavity. The waggle portion of the dance involves the bee moving in a certain direction while wagging her body from side to side and vibrating her wings to produce a buzzing sound. At the end of each waggle run, the bee circles back to her starting point, alternating between clockwise and counter clockwise turns such that each two successive rounds create a figure eight (Figure 1a). The angle of the waggle run relative to the upward direction indicates the angle of the flower patch relative to the sun's position in the sky, and the duration of the waggle is positively

correlated with the distance to the flowers (Figure 1b). Finally, the overall number of waggle runs is positively correlated with relative food quality. Typically, a few observer bees closely attend to the dancer's movements and are exposed to any floral odors carried on her body.

A variety of experiments, as well as recent observations using harmonic radar, indicate that observer bees learn the direction and distance information encoded in the waggle dance and rely on that knowledge to arrive in the general vicinity of the indicated patch of flowers. The bees are further assisted in locating food by olfactory and visual cues from the flowers and perhaps also by directly following model bees or homing in on pheromones that other foraging bees emit. Honeybees also rely on waggle dances to inform hive mates about other resources (such as water) as well as potential new nest sites when the colony swarms.

Although the waggle dance was not originally described as such, it meets three commonly agreed upon criteria for the identification of teaching. First, the teacher should incur some cost. The model bee spends time and energy on the dance and pays an opportunity cost involved in delaying her return to the rich flower patch about which she is dancing. Second, teaching of a given task should be performed selectively only in the presence of individuals not familiar with that task. A returning forager performs the waggle dance based on her assessment of both the patch and colony needs, and the sole function of the dance is to recruit bees unfamiliar with a given flower patch to it. Third, the pupil should benefit from the teaching. Critical experiments indicate that inexperienced bees can find a flower patch much faster after attending to waggle dances coding its location. Finally, an implicit assumption about teaching is that the pupil has learned new information that guides its future behaviour even in the absence of the teacher. In honeybees, new recruits first learn the dance information, which enhances their initial arrival in a flower patch. They then learn landmarks associated with that patch and can subsequently locate it on their own. Furthermore, recruits to a patch can code this newly acquired information about flower location in their own waggle dances, if they choose to perform them.

Unlike the waggle dance in bees, tandem running in ants, among the simplest means of conveying social information, has been formally described as teaching. Tandem running involves a successful forager leading a recruit from their nest to the food site. Here, the teacher adjusts her behavior to ensure that the recruit follows her. Such adjustment lengthens the teacher's travel time. The recruit, however, arrives at the food faster than she would on her own, and she can find the food independently in later trips.

Between the extremes of advanced waggle dances and simple tandem running, social hymenoptera exhibit a variety of means for conveying information to nestmates. Many but not all of these mechanisms of social communication may be classified as social learning. For example, stingless bees (tribe Meliponini), among the closest relatives of honey bees (tribe Apini), consist of over 450 species found mostly in the Neotropics. In most of the species that have been examined, successful foragers display behaviors similar to those of honeybee dances. The dances are followed by recruits that then leave the nest in

search of food. Some species rely heavily on scent trails leading to the food whereas others, such as *Melipona panamica*, seem to communicate distance and height of a food via sound. In *M. panamica*, no feature of the dance is correlated with the food direction, leading to the suggestion that observers directly watch the departing model and follow her in the direction of the food. All social hymenoptera studied exhibit excellent individual learning, so it is likely that when observers respond to social signals by traveling to a food source they learn where the food is located so they can find it later for themselves.

Choice and handling of flowers

In addition to recruiting nestmates to distant food sources, social bees can also copy the flower choices of experienced foragers. In one study with bumblebees (*Bombus terrestris*), each trial was initiated by allowing a demonstrator bee to forage on an inflorescence consisting of artificial flowers in an arena containing four yellow and four blue inflorescences that were equally rewarding. Then an inexperienced observer bee was introduced into the arena. The observer bees showed a significant preference for landing on the occupied inflorescence rather than unoccupied ones and, on subsequent foraging trips in the absence of the demonstrator, exhibited significant preferences for inflorescences of the same color on which their demonstrator had been observed.

Social learning may also influence bees' handling of flowers. 'Nectar robbing' bees either punch a hole at the base of a flower or use holes previously punched by other bees to extract nectar rather than access the flowers legitimately, in the way that facilitates pollination of the flower. Observer bees (*B. terrestris*) that extracted nectar from flowers with holes previously punched by model bees were thereafter more likely to punch holes in intact flowers than were control bees with no prior nectar-robbing experience.

Conclusions

Research on insect social learning is still in its infancy. It is already clear, however, that some insect species rely on social learning to guide their behavior. The types of information learned from others can be rather minimal, as in the case of odor cues remaining from the larval period, which can help newly eclosed adult insects chose their own egg laying substrate, or sophisticated as in the honeybee waggle dance, which involves symbolic coding of environmental features. It is likely that many cases of insect social learning remain to be discovered whereas others, such as the forms of social learning about food sources within the numerous species of stingless bees (Meliponini), require further study to be fully understood.

Some features of insect life history, including lack of parental care and non-overlapping generations, could limit the prevalence of social learning. However, other attributes of insects, most notably their sheer diversity and the high level of social behavior seen in some species, could allow for the evolution of intriguing forms of socially acquired information.

Further reading

- Dukas, R.** 2008. Evolutionary biology of insect learning. *Annual Review of Entomology*, 53, 145-160.
- Dukas, R. & Ratcliffe, J.** (Eds) 2009. *Cognitive Ecology II*. Chicago: University of Chicago Press.
- Dyer, F. C.** 2002. The biology of the dance language. *Annual Review Entomology*, 47, 917-949.
- Holldobler, B. & Wilson, E. O.** 1990. *The Ants*. Cambridge, Mass.: Harvard University Press.
- Leadbeater, E. & Chittka, L.** 2007. Social learning in insects - From miniature brains to consensus building. *Current Biology*, 17, R703-R713.
- O'Neill, K. M.** 2001. *Solitary Wasps: Natural History and Behavior*. Ithaca, NY: Cornell University Press.
- Prokopy, R. J. & Roitberg, B. D.** 2001. Joining and avoidance behavior in nonsocial insects. *Annual Review of Entomology*, 46, 631-665.
- Seeley, T. D.** 1996. *The Wisdom of the Hive*. Cambridge, MA: Harvard University Press.
- von Frisch, K.** 1967. *The Dance Language and Orientation of Bees*. Cambridge, MA: Harvard University Press.

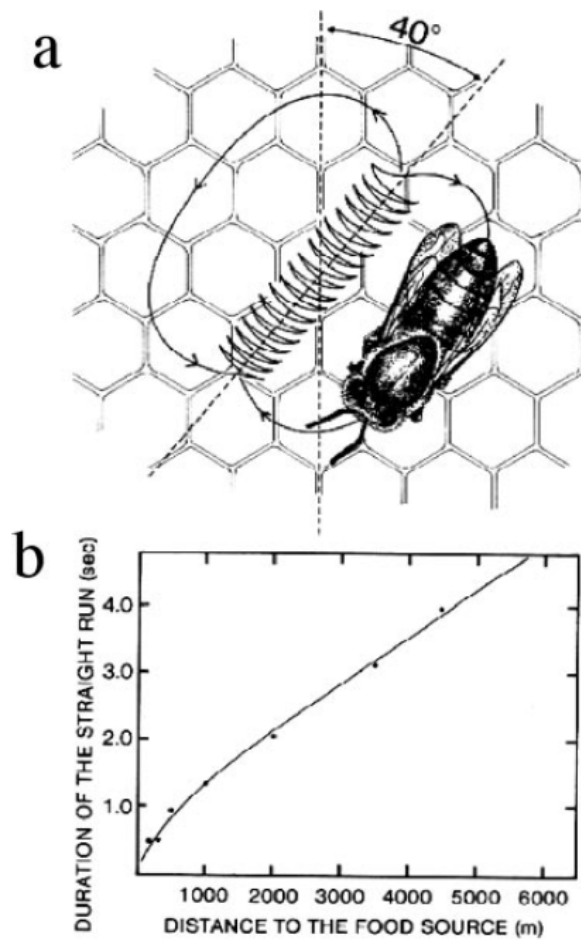


Figure 1. (a) The waggle dance of honeybees. In this example, the angle of the waggle run is 40° relative to the upward direction, meaning that the food source is 40° relative to the sun's current position in the sky. (b) The duration of the waggle run is positively correlated with the distance to the food source. Reprinted, with permission, from the Annual Review of Entomology, Volume 47 ©2002 by Annual Reviews www.annualreviews.org.