

Social Learning in Insects – From Miniature Brains to Consensus Building Review

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Communication and learning from each other are part of the success of insect societies. Here, we review a spectrum of social information usage in insects – from inadvertently provided cues to signals shaped by selection specifically for information transfer. We pinpoint the sensory modalities involved and, in some cases, quantify the adaptive benefits. Well substantiated cases of social learning among the insects include learning about predation threat and floral rewards, the transfer of route information using a symbolic ‘language’ (the honeybee dance) and the rapid spread of chemosensory preferences through honeybee colonies via classical conditioning procedures. More controversial examples include the acquisition of motor memories by observation, teaching in ants and behavioural traditions in honeybees. In many cases, simple mechanistic explanations can be identified for such complex behaviour patterns.

Introduction

The study of social learning — how animals obtain information by extracting it from other animals — has almost entirely focussed on the vertebrates [1–7]. However, the first published description of animals learning through observation of others, dating to Darwin, relates to pollinating insects; honeybees ‘imitating’ bumblebees’ techniques of nectar-robbing by cutting holes into flower spurs and extracting nectar without pollinating the flowers:

“I think the hive bees either saw the humble bees... and understood what they were doing ...; or that they merely imitated the humble bees...” [8]

“...should this be verified, it will, I think, be a very instructive case of acquired knowledge in insects. We should be astonished did one genus of monkeys adopt from another a particular manner of opening hard-shelled fruit; how much more so ought we to be in a tribe of insects so pre-eminent for their instinctive faculties, which are generally supposed to be in inverse ratio to the intellectual!” [9]

Darwin’s conjectures about bees copying nasty habits from other pollinators are highly unusual in several respects. He credits insects with considerable cognitive abilities at a time when many biologists considered them to be little more than simple reflex machines. We now know that insects, especially bees,

have a variety of impressive cognitive skills, including object categorisation, the ability to learn about abstract concepts and the ability to solve context-dependent problems [10–12]. However, owing to their small brain size, the study of insect learning has a good tradition of deconstructing seemingly complex phenomena and explaining them in terms of simple processes [13]. This strict necessity to look for the most parsimonious explanation when dealing with insects provides an ideal perspective from which to study the mechanisms of social learning, too.

Of course, Darwin’s observations most likely reflect much simpler mechanisms than the explanations that he offers. We nonetheless agree with Darwin’s apparent assessment that insects — particularly social insects — might provide a promising system to study social learning. Many insects are pollinators, who must compare the nectar and pollen offerings of different plant species and attempt to find the best bargains [14]. Gaining reliable information on what constitutes a good flower species or patch often requires extensive sampling [15]. As many species of pollinators often work concurrently in a meadow, there is ample opportunity for picking up information from others. Moreover, social insects live in colonies of hundreds to thousands of highly related individuals. Accurate information about environmental conditions is required to achieve optimal task allocation, but sometimes the individuals that carry out these tasks never have even left the nest [16]. In these ‘superorganisms’ there is perhaps a need for active information sharing and learning from each other that is unparalleled in the vertebrate world.

A third unusual aspect of Darwin’s observations is that he thought it apparently natural that behavioural patterns might be copied not just within, but across species. During a century of research on social learning, the focus has been largely on interactions between conspecifics. Examples of studies on learning from members of other species are rare, e.g. [17–19], yet, there is no *a priori* reason to treat those cases differently. In fact, where resources are shared or where generalist predators lurk, picking up information from heterospecifics may be just as valuable as from members of the same species.

We describe below a spectrum of social information use in the insects. In some cases, insects make use of social information that is inadvertently provided by others; in other cases — notably within the social insects — they invest considerable effort into passing on learnt information. The value of the information obtained from others depends on context [20], and insect social learning systems are often flexible enough to ensure that individuals rely on social information only when individual learning will not suffice or learn only from individuals that bear the most valuable information. We hope that, although we focus on creatures with miniature brains, our approach may be of value to the study of social learning in other organisms.

Box 1

Social learning glossary.

Exposure: Through interaction with a conspecific, an animal is exposed to the same learning environment and, therefore, acquires the same behaviour pattern more quickly than it would on its own.

Imitation: Copying of a demonstrator's body movement or motor pattern by an observer.

Inadvertent social information: Social information that is provided as a coincidental by-product of an animal's behaviour.

Local/stimulus enhancement: An animal is attracted to a particular location or object through cues associated with the presence of a conspecific. These processes may give rise to learning, if the observer learns something as a consequence of gaining access to that particular stimulus.

Matched-dependent learning: An observer learns that the behaviour of another animal predicts a particular outcome, which may additionally facilitate learning of non-social cues which predict the same.

Observational conditioning: A classical conditioning process in which animals initially produce a learned or unconditioned response to a social stimulus and later learn to produce the same response to a conditioned stimulus that has been paired with the same unconditioned stimulus.

Public information: A subset of inadvertent social information. Public information is provided when the behaviour of one animal makes certain environmental cues available to another.

Signal: A behaviour pattern or physiological trait which has been shaped by selection specifically because it functions in communication.

Social cues: A subset of inadvertent social information whereby an animal's behaviour reveals the conclusions that it has drawn through sampling that site.

Social learning: Classically defined as "learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products" [38]. Social learning should not be confused with 'learning by groups' or societies as a whole. Rather, it is learning by individuals that takes place in a social context.

Inadvertent Social Information

It has long been recognized that social interactions offer animals the opportunity to update their knowledge of the environment by observing the behaviour of others. Most authors distinguish between two forms of social learning, based on the role of the animal that originally possesses the information [3,21,22]; individuals actively share environmental information via specific signals or they produce inadvertent social information [3] (Box 1). We first describe several cases of the latter.

Learning about Foraging Options: Location Cues

The presence of a foraging conspecific may provide valuable information as to the location of a potential feeding site. However, for the many insects that forage upon small resources, such as flowers, such information may be of limited value because using it inevitably involves depletion of that resource. How do insects balance the need to identify new food types against the disadvantages of visiting relatively low-profit resources? A number of studies have suggested that insects may use conspecific presence to identify an unfamiliar feeding site, but ignore social information once they are familiar with the characteristics of that resource, e.g. a flower species that can subsequently be identified also at different locations.

When bumblebees (*Bombus terrestris*) visit an unfamiliar flower species for the first time, they show a significant tendency to land on occupied flowers, suggesting that conspecific presence may attract them towards potential food resources [23–25]. As a result, foragers take significantly less time to probe unfamiliar flowers when conspecifics are already foraging there [24]. However, once bees have probed these flowers,

and thus learnt about nectar availability and quality, they no longer prefer occupied flowers and decide for themselves about which ones to visit [23]. In the wasp *Vespula maculifrons*, the role of experience has not been evaluated directly, but differences between the results of various studies are highly consistent with such an effect [26]: when naïve foragers were tested, individuals show a preference for occupied food sites [27], but when wasps were experienced with the resources they visit, they avoided conspecifics [28,29].

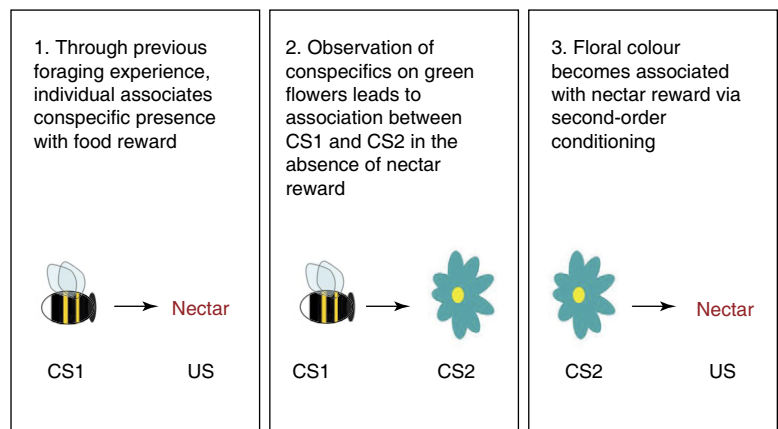
In some stingless bee species, foragers already possess information as to the general location of food sources, because nestmates leave scent trails which guide others to the correct place [30]. However, individuals have no experience of the physical features of a food source until they have visited it. In the stingless bee *Trigona amalthea*, the presence of a foraging conspecific rendered particular nectaries attractive to naïve foragers [26]. However, when bees subsequently returned to the flowers to collect more nectar, this attractiveness disappeared quickly, and regular visitors to the patch avoided the occupied nectary. The presence of conspecific foragers may thus allow naïve individuals, who may have been recruited to the flower site, to narrow down the precise location of the nectar source. Newly recruited honeybees also use the presence of conspecifics to identify food resources, even though they often possess information about the general location of food from inside the nest [31].

Learning about Foraging Options: Colour/Visual Cues

Flower colour is an important cue used by bees to memorise and identify rewarding flower species [32,33]. Bees learn about flower colours through

Figure 1. Social learning processes akin to second-order conditioning in bumblebees.

A seemingly complex behaviour — copying the flower choices of other bees — could emerge from simple associative learning, whereby foragers use the appearance of conspecifics as prediction of reward.



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simple associative learning, whereby colour must be paired with a reward in a critical time window [34]. Very few trials are necessary to establish a durable memory trace [34,35]. What role does social information play in the decision to sample a particular flower species? Two recent studies have shown that bumblebees appear to copy other bees' learnt foraging preferences. *Bombus terrestris* foragers will abandon an unrewarding species, and switch to a better alternative more quickly when accompanied by experienced workers [36]. In another study, *Bombus impatiens* workers appeared to learn by observation, rather than just being attracted to conspecifics. Demonstrators foraged from green rewarding flowers, whilst avoiding orange alternatives [37]. Bees from another colony were able to observe the foragers through a screen, without sampling the flowers or interacting directly with conspecifics. These individuals were subsequently offered the choice between orange and green flowers in the absence of demonstrators. They showed stronger preferences for green than non-observing controls or than bees that had observed conspecifics on orange flowers, indicating that floral preferences were enhanced simply by seeing a conspecific on flowers of that type.

While this behaviour qualifies as social learning, as the previously naïve observers have learnt through observation of the behaviour of conspecifics [38], there are several possible mechanistic explanations. One possibility is stimulus enhancement (Box 1); alternatively, the mechanism might be a relatively simple form of associative learning. Bees are capable of second-order conditioning, whereby an unconditioned stimulus (US; such as a sucrose reward) is associated with a conditioned stimulus (CS1; e.g. a visual signal), and this CS1 also becomes associated with a second stimulus (CS2; e.g. another visual signal). The CS2 can subsequently be used to predict the reward, even in the absence of the CS1 [39] (Figure 1). As the observer bees had previously foraged together with conspecifics on artificial flowers, they may have simply learnt that the presence of another bee on a flower is a first-order predictor of reward (CS1). In the training, conspecifics (CS1) could be observed foraging on green flowers; thus, the observers could have learnt to associate the CS1 with the CS2, and

subsequently could have used the green colour to predict reward (cf. Heyes' [38] definition of observational conditioning).

Note that the CS1 here does not have to be a conspecific: it could be an insect of a different species, a scent or a landmark next to the target. Bees can learn to associate even fairly arbitrary visual stimuli, for example, human faces [40], with a reward. Alternatively, it is possible that conspecifics have a stronger influence — after all, most animals can recognise conspecifics — but we need more data to establish whether this is the case. Although the role of associative learning in the *maintenance* of socially-learned behaviours has been a focus of attention in the social learning literature [41,42], the role of learning in the *development* of social cue use is sometimes not fully explored (but see [43]). For example, octopuses that have observed conspecifics attacking red balls also attack red balls in preference to white alternatives and vice versa [44]. It is clearly possible that these subjects may have learnt to associate conspecifics, especially those exhibiting attack behaviour, with food, and that this CS1 becomes associated with the CS2 of colour. Second-order conditioning, or higher-order observational conditioning, does not require that any special relevance is attached to the CS1 simply because it is a conspecific.

Learning about Foraging Options: Chemosensory Cues

Rats can find out about the food a conspecific has ingested by sniffing each other's breath and will later prefer food that emanates the same scent [6]. A similar phenomenon, albeit with different underlying mechanisms, is found in bumblebee colonies [45]; when successful foragers bring home scented nectar, other colony members will later prefer the same type of food. In bumblebees, the explanation is simple, because the foragers deposit the scented solution in honey pots, where 'observer' bees are free to sample it. If suitable, these bees will associate the scent with food by simple classical conditioning. Note that the learning process in rats requires a distinct social cue — carbon disulfide in the rats' breath [46], — whereas this might not be the case in bumblebees, who learn the floral scent in the hive individually. In honeybees and stingless bees, such transfer of olfactory preferences is also known,

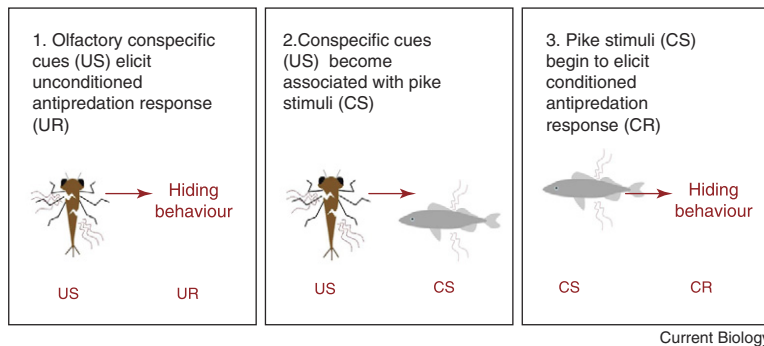


Figure 2. Classical conditioning by conspecific cues in damselfly larvae.

Juvenile damselflies can learn from conspecifics to avoid predation. This can be explained by simple associative learning without the need for higher order cognitive processing.

but here it is based on active dissemination of scent information in the hive [47] and will thus be discussed later.

Scent cues left at resources by previous visitors represent possibly the most diverse form of social information during insect foraging. These chemical deposits appear to function both when foragers recruit others to food sources, and when individuals need to avoid depleted, small scale resources. Foraging honeybees and bumblebees leave traces of volatile chemicals on the flowers that they visit and such marks can elicit avoidance behaviour in conspecifics [48–50]. This behaviour was thought by some to be an adaptation which allows the marker, or even its nestmates, to avoid revisiting the same flowers. However, in *Bombus terrestris*, the chemical composition of the scent marks are identical to the chemical ‘footprints’ that these bumblebees leave everywhere they walk [51]. These footprints probably represent the same cuticular hydrocarbons that are passively secreted by the bumblebee cuticle and also protect against desiccation and aid adhesion to smooth surfaces [51]. Thus, it seems likely that in bumblebees such olfactory cues may represent a source of inadvertent social information rather than a signal.

It has become clear that scent marks do not simply elicit avoidance or attraction behaviour, but that foragers learn about how to use them and vary their behaviour according to context. Bees learn to use scent marks as an attractive rather than repellent stimulus, if they are consistently associated with reward [52]. In line with the prediction that the benefits of relying on social information use should depend upon the costs of individual sampling [20,53], bees respond to the marks more when the time costs of mistakenly choosing a depleted flower are high [54].

These scent cues also provide a spectacular case of how valuable information is used between species: the solitary wool-carder bee *Anthidium manicatum* avoids flowers that have been scent-marked by the bumblebee *Bombus terrestris*, and vice versa [55]. *B. hortorum*, *B. pascuorum*, *B. pratorum* and *B. terrestris* all avoid each other’s scent marks [49]. Bumblebees avoid flowers recently visited by honeybees and vice versa [50], as well as rejecting those visited by hoverflies [56]. Perhaps the most dramatic example occurs in the stingless bee *Trigona spinipes*, where foragers ‘eavesdrop’ upon the scent trails of *Melipona*

competitors and subsequently take over that food source by either killing or driving away the unlucky original finders [57].

Learning about Predation Threat

Avoiding predators seems a particularly adaptive application of social information use and some of the most convincing evidence of insects social learning comes from predation. Damselfly larvae (*Enallagma boreale*), which are preyed upon by pike, can rapidly acquire the ability to recognise local predation risk based on both conspecific and heterospecific cues [58] (Figure 2). Pike-naïve larvae, which do not respond to olfactory cues from pike predators, reduced their feeding activity and movement when presented with a combination of pike stimuli and chemical cues from injured conspecifics. When the same individuals experienced pike stimuli one day later, in the absence of any conspecific cues, they again changed their behaviour and became less active, implying that an unconditioned response (anti-predator behaviour) to an unconditioned stimulus (cues from injured conspecifics) had become conditioned to a new stimulus (pike cues). Thus, the damselflies had learnt specifically about a local predator through the fate of their conspecifics. This could be attributed to a classical conditioning process whereby an unconditioned response (hiding) to an unconditioned stimulus (cues from injured conspecifics) becomes associatively conditioned to a new stimulus (pike cues) — a process called ‘observational conditioning’ [59] (Box 1). As observational conditioning does not require that the observer draws any inference about the demonstrator’s reaction [60], similar processes might occur in any organism that can learn in a simple Pavlovian manner.

Juvenile wood crickets (*Nemobius sylvestris*) can learn to respond to predation threat through the behaviour, rather than the fate, of their conspecifics. Inexperienced crickets were placed in leaf-filled boxes, accompanied by conspecifics that either had not recently interacted with predators or that had recently experienced a high predation threat and were accordingly tending to hide under the leaves [61]. Observers whose companions had been exposed to the dangerous environment were later themselves more likely to be found hiding than those whose companions had no recent predator experience. These behavioural differences could still be observed even 24 hours after removal of the demonstrators. Thus, 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.

It is interesting to speculate what cues the observers actually used to gauge predation threat. One possibility is that observer crickets were joining experienced crickets by simple local enhancement: if more crickets are under leaves, the probability of randomly encountering another cricket under a leaf is higher than encountering one on top of the leaf. The inexperienced crickets might simply have maintained their 'submerged' position after the demonstrators were removed, without actually 'understanding' that there was a predation threat. When the authors simulated a non-predatory disturbance which led crickets to shelter under the leaves, their subjects emerged much sooner, suggesting that the crickets' tendency to remain in the same place cannot fully explain their findings [61]. Either way, the observer crickets had clearly changed their behaviour as a result of demonstrator behaviour, resulting in an adaptive response to predation threat.

Using Signals to Transfer Learnt Information

Animals might be expected to provide inadvertent social information in a wide range of social contexts, from situations where they profit substantially by doing so, to those where they incur no benefit or even some cost [3]. In contrast, theory would suggest that actively sharing information about the environment by signalling should evolve only when the signaller incurs significant fitness benefits, either directly or through inclusive fitness [62]. The unique life histories of social insect colonies, where foraging is often co-operative and individuals live in tight proximity to closely related kin, should thus nurture the evolution of signals and indeed does so (e.g. [30,31,63]).

Classical Conditioning in Nature: Trophallaxis in Bees

In honeybees, von Frisch [31] was the first to suggest that foragers may be attracted to the same flower species that their nestmates have successfully foraged upon through social information about floral scent. Von Frisch hypothesized that successful foragers may play an active role in this phenomenon because they transfer samples of liquid food to others inside the hive via trophallaxis [31]. During a trophalactic interaction, a successful forager proffers samples of regurgitated nectar, whilst the recipient inserts her proboscis into the donor's mouthparts (Figure 3) [64].

Using the proboscis extension-reflex paradigm, it was demonstrated that bees learn associations between floral scent and nectar rewards during trophalactic interactions, just as they would were they to sample the flowers themselves [47,65]. Even after a very brief food exchange, contact with an airflow containing the same floral scent triggers proboscis extension, indicating that an association has been learnt between a floral scent (the unconditioned stimulus) and a nectar reward (the conditioned stimulus). As trophallaxis between a dancing bee and its followers is common, it is likely that this information allows recruits to seek



Figure 3. Trophallaxis in a honeybee colony.

The donor (left) opens her mandibles to proffer samples of regurgitated nectar, whilst the recipient inserts her proboscis. Photograph by C. Grüter.

the nectar source that the dancer has found to be profitable.

Farina *et al.* [66] also suggest another intriguing, but as yet untested, possibility. Trophallaxis occurs between foragers and younger receiver bees, whose task is nectar processing within the hive, but who become foragers later in life. As the memories established via trophallaxis can be relatively long-term [47,65], the information acquired may lead to food preferences once these bees become foragers. This would mean that young bees obtain information from older, experienced individuals. However, this does not require that more seasoned bees are identified as such, instead it is a simple by-product of age polyethism — the phenomenon that honeybees divide labour according to age, such that younger bees attend to tasks within the hive and older bees forage [31].

Learning the scent of rewarding flowers through trophallaxis provides a clear example of how transmitter individuals can bring about learning of an association between two stimuli simply by bringing the receiver into contact with them. In fact, actively promoting learning in this way might even be described as 'teaching', as it fulfils criteria of teaching in non-human animals [67].

Teaching in Honeybees and Ants?

Teaching in non-human animals is usually differentiated from other forms of communication on the basis of three minimum criteria, as defined by Caro and Hauser [67]. Teaching must exert a cost, or at least confer no immediate benefit, on the 'teacher'. The candidate behaviour must be performed only in the presence of potentially naïve individuals and not broadcast on the basis that other animals may potentially come across it. Finally, teaching must lead the 'pupil' to acquire knowledge earlier than it would otherwise.

Many ant species exhibit a complex recruitment strategy, known as 'tandem running' (Figure 4), which has been suggested to qualify as teaching [68]. During a tandem run, an ant that has found either a food source that it cannot effectively exploit alone or a potential nest site leads a follower to the site, stopping and displaying a calling behaviour if the recruit loses antennal contact [63]. The leader incurs a cost through guiding her follower, as she reaches food sources on average four times more quickly when

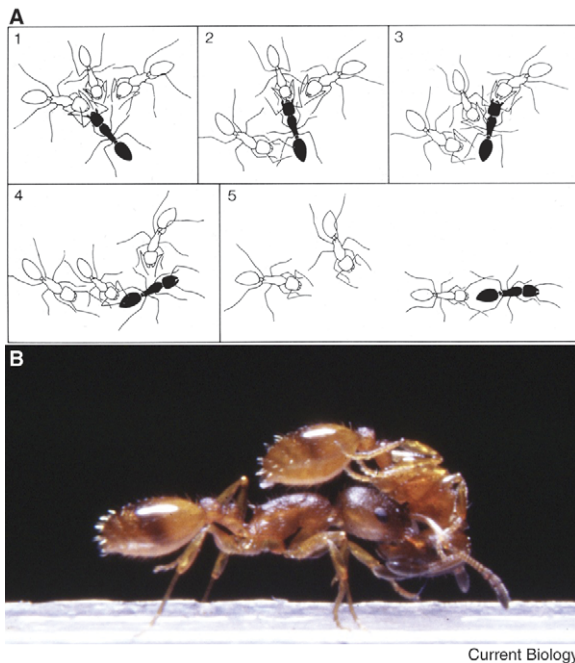


Figure 4. Tandem running and transport in ants.

(A) Recruitment to a food source via tandem-running in *Campoplex sericeus*. A tandem leader (black) recruits potential followers (white) via food-offering rituals. Many ants attempt to keep antennal contact with the leader, but when she finally leaves the nest, only the ant in closest contact is successful. The tandem run proceeds to the food site, unless antennal contact is broken. Figure reproduced with permission from Figure 7-51 in [63]. (B) Transporting nestmates to a target is faster than tandem running, but recruits are carried upside down, facing backwards, and thus are unlikely to learn about the route along which they are carried. Photograph by Stephen Pratt, reproduced with permission from [88].

alone; furthermore, the behaviour is dependent upon the follower's presence given that the leader will not proceed unless antennal contact is maintained [68]. It remains to be shown that the location of the target site is learnt by the follower in a foraging context, but when tandem-running occurs during nest-site recruitment, tandem followers often return to their colony to lead other recruits to the same site, implying that learning does take place [69]. In fact, tandem-running during nest site recruitment provides a fascinating example of how trade-offs between the costs and benefits of teaching lead to different behavioural strategies. Scouts that initially find a nest site will lead a small number of tandem followers to it whilst the site is empty, but once the pool of ants that have learnt the route reaches a threshold, they switch to simply carrying the rest of their nestmates to the site [70]. Transport proceeds three times faster than tandem running, but carried recruits do not learn which path to take because they are transported upside down and thus cannot recruit others (Figure 4) [70].

Trophallactic interactions between honeybee foragers meet Caro and Hauser's [68] three criteria: the donation of food is carried out only in the presence of a receiver, the donor does not benefit immediately — she even sacrifices a portion of her harvest — and the

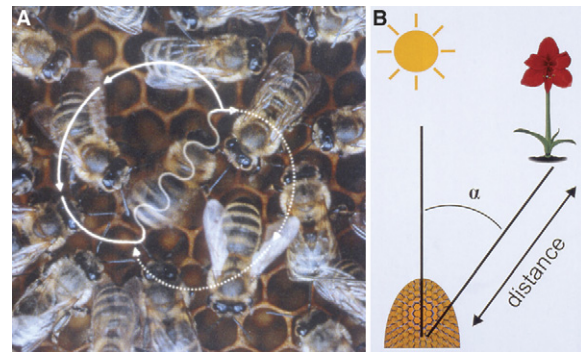


Figure 5. The honeybee dance language.

(A) Figure-eight shaped waggle dance of a honeybee on the vertical comb. The direction of the waggle run (wavy line) relative to the direction of gravity corresponds to the angle between the sun's azimuth and the indicated food source outside the hive (B). The duration of the waggle reflects the distance of the food from the hive. Reproduced with permission from [103], designed by J. Tautz and M. Kleinhenz.

recipient learns about which flower species are currently producing nectar. Perhaps the most thoroughly researched form of communication in insects is the honeybee dance language (Figure 5). The dances are rarely discussed in the context of social learning, and yet, recruits clearly learn and apply the information provided by dancers [31]. The waggle dance is thus also likely to qualify as teaching, although a direct demonstration that the behaviour is exclusively performed in the presence of naive observers is missing. However, we suggest that the term 'teaching' be reserved for transfer of skills, concepts, rules and strategies — not simply the handing over of declarative or procedural information [71].

Behavioural Traditions in Honeybees?

So far, we have highlighted the role of social learning as a means to rapidly track short-term changes in the environment, such as temporary foraging bonanzas or local predation threats. By nature, these behavioural changes are transient; indeed, it is precisely because environments change rapidly and unpredictably that this horizontal transmission of behaviour may be adaptive [72]. However, such short-term responses are notably different from the long-term, crossgenerational social habits that we call 'traditions' and that are typified by variation in primate or avian tool use and foraging techniques or songbird dialects [73–75].

Traditions in invertebrate behaviour have received little attention (although see [76]), perhaps because they are considered to be the building blocks of cultural phenomena [77], which seem a far cry from such small-brained creatures. But although the learning processes which support culture itself may be highly sophisticated [4,78], there is little reason to suppose that insects do not possess the learning abilities required to support long-term behavioural change. Many adult plant-eating insects exhibit a strong preference for the food they experience as larvae [79,80], even though the insect nervous system is extensively remodelled during metamorphosis [80]. These preferences can thus lead to transmission of

food preferences from parents to offspring, even when the species as a whole is a generalist [81]. Thus, it is certainly true that insect larval conditioning can lead to strong and persistent learning about environmental features. Might long-lasting behavioural changes also be induced in larvae by social cues [82,83].

Kirchner [83] explored whether the daily rhythm of a honeybee colony's activities could be learnt by foragers that do not directly experience circadian changes in food availability. He trained groups of foragers that food was available for only one hour a day, either early in the morning, at midday, or in the evening. These bees learned to match their activity pattern to the availability of food (Figure 6). Brood cells were then removed from each colony, and larvae developed into adults in an incubator, without contact with their older nestmates. After hatching, these bees' preferred activity patterns matched those of their mother colonies (Figure 6). The exact mechanism by which the young brood becomes conditioned to the colony's activity period remains a mystery, but Kirchner favours the hypothesis that increased levels of vibrational signalling on the dance floor during periods of heavy recruitment may be responsible [83].

It remains to be shown whether this type of learning of activity patterns remains stable over time, or whether such preferences disappear as bees gain experience with their environment. Furthermore, this phenomenon does not represent learning across true biological generations, because the young workers will be the younger sisters of the older cohort of foragers, unless the old queen has been replaced. However, these findings suggest that the potential for longer-term social learning, if not tradition, certainly exists. Honeybee colonies survive for an average of 5.6 years at the same site under successive queens, if they make it through the first winter [84]. Theory suggests that this type of life-history, where environments fluctuate over the course of a few generations, should favour the evolution of social learning because it allows for greater phenotypic flexibility than genetically inherited information, but avoids the costs of individual learning [53,85].

Putting Social Information to Adaptive Use

A recurring theme of the examples above is that insects — like other animals [20] — rarely tend to rely entirely on social information. Using the findings of others to guide behaviour may offer a more economical alternative to individual sampling, but the relative costs and benefits of either strategy are rarely made explicit. In fact, theory predicts that social information use will pay off under a relatively limited range of circumstances, especially if it precludes individual sampling [86]. For example, although it might intuitively seem that learning from others about where they have found food must increase foraging efficiency, in practice the costs of waiting for such information might often outweigh the benefits [87], especially if all foragers choose to wait for social information rather than individually discovering new food patches. How do insects capitalize upon the potential benefits of using social information, whilst avoiding the pitfalls?

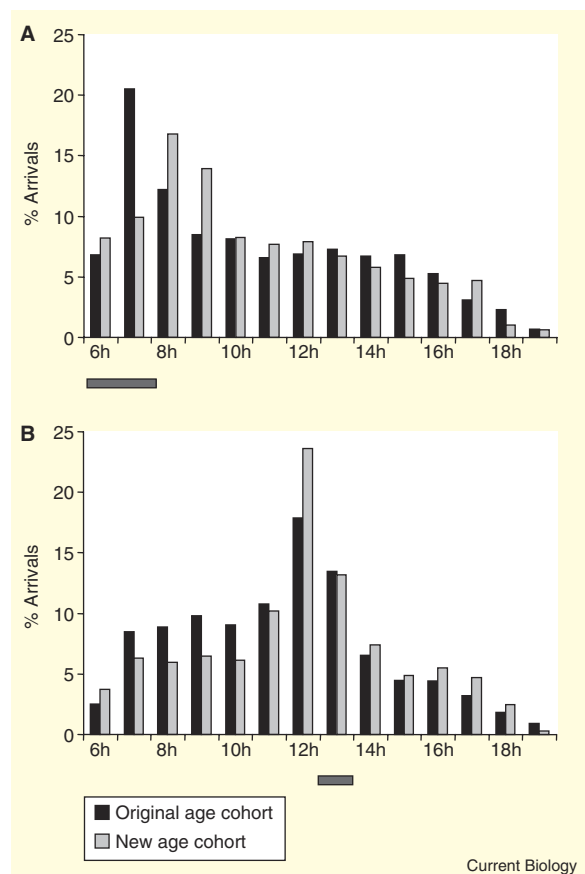


Figure 6. Tradition in the honeybee hive?

Bees of the 'older generation' (black bars) were offered feeders either early in the morning (A), or at midday (B) (indicated by black bars beneath the abscissa). These bees clearly learnt to concentrate the foraging efforts at the correct time of day. Brood combs containing larvae or pupae while the 'older generation' foraged were removed, and the 'young generation' subsequently raised in incubators, removed from their experienced older hive mates. Even though this new cohort of bees had not been entrained a schedule by the experimenter, foragers nonetheless displayed the same temporal activity pattern as the older cohort (grey bars). Control colonies with no trained groups showed continuous foraging throughout the day. Data from [83], redrawn with permission from W. Kirchner.

Avoiding Informational Cascades: Deciding Where to Live

Perhaps one of the greatest challenges facing social insect colonies is that of moving house. In ant colonies and honeybee swarms [88–90], between a hundred and several thousand individuals move in synchrony from their old home into the best of a range of potential new nest sites. They are guided by a small minority of scouts, who reliably reach a consensus as to the highest-quality site [91] through an intricate combination of social and individual learning, even though each individual rarely samples every option for itself [90,92].

Honeybee scouts share nest-site information via waggle dances. A scout within a swarm (which will cluster on a tree branch for hours during the decision-making process) learns about both the location

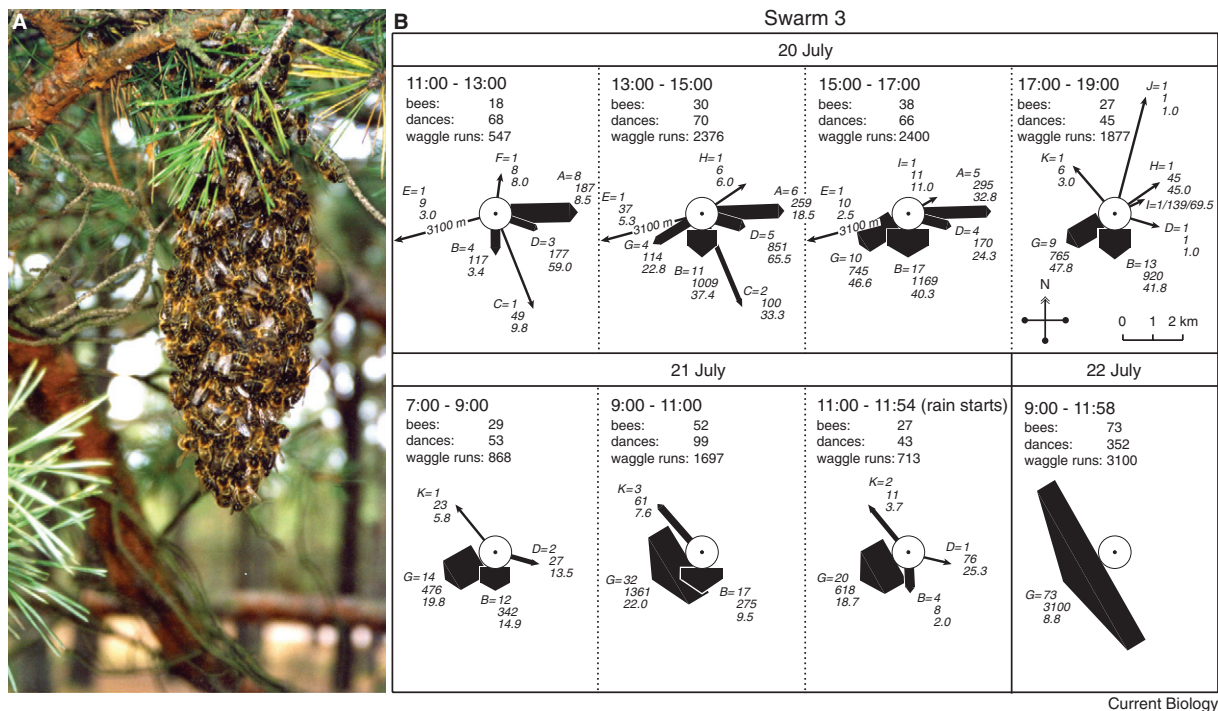


Figure 7. Honeybee swarming.

(A) A honeybee swarm clustered on a tree branch (photo by R. Sachs). Swarm sites such as this can persist upwards of three days, during which time scouts investigate potential sites and communicate their findings by dancing on the swarm's vertical surface. (B) Decision-making in a honeybee swarm, from the time when the first potential nest site was advertised until eventual lift-off. Circles represent the location of the (stationary) swarm; arrows indicate the direction of the nest site; width of arrows indicates the number of bees dancing for that nest site in the time period shown. The numbers associated with each arrow represent the total number of bees dancing for a site (top), the number of waggle dances performed for a site (middle) and the mean number of waggle runs per site (bottom). Numbers in the top right corner of each box are totals for that time period. Reproduced with permission from [104].

and quality [90,92] of one particular site by following the dance of another returning scout, just as she would learn about food location by following the dance of a forager. After visiting the site herself, she begins to dance, performing more intense dances for higher-quality sites [90,92] and recruiting other scouts from the pool of dance followers. Clearly, if this process were to continue indefinitely, a stalemate would result, with different cohorts of dancers resolutely dancing for different sites. However, scouts gradually reduce the intensity of their dances, and eventually abandon them, subsequently following another, randomly chosen dance [93]. Because the duration of dancing is longer for high-quality sites [90,92], the result is a gradual accumulation of bees dancing for the best sites, and eventual unanimous dancing for one site alone (Figure 7). Note that this results in a seemingly highly advanced pattern — individuals specifically learn more from scouts that have the more valuable information; but this does not require that such scouts be identified, nor that the information provided by different scouts is even compared by observers. Instead, because scouts that have found a particularly suitable site exhibit more prolonged dances, it is simply more likely, by probabilistic processes, that an information-seeking bee 'bumps into' a scout indicating a top-quality site [90,92].

An essential feature of nest-site selection is that bees independently verify what they have learnt

socially by visiting the site themselves. Returning scouts provide their dance followers with information about where a site can be found and a subjective assessment of its quality, but observers following a dance have no access to the site itself at this point. If animals base their decisions entirely on the 'conclusions' of others [3], they may fall victim to erroneous informational cascades when demonstrators make inappropriate judgments [17,94]. In this case, such a mistake could result in the entire colony migrating to a poor site. Thus, individual inspection of the sites found by others, rather than blind copying of the outcome of decisions, ensures that mistakes are unlikely to initiate a cascade of misplaced support [89].

Using Social Information When Personal Information Will Not Suffice

In birds, fish and mammals, empirical data support the prediction that animals value individually obtained information above social cues, if it is available and reliable [20,95]. Evidence from insects also suggests that social information is often used as a back-up, if no other cues are available or if their own information has proved unreliable. For example Mediterranean fruit flies *Ceratitis capitata* prefer to oviposit where other females can be found if offered visual but not olfactory fruit mimics, but are not influenced by their conspecifics' choices if scent cues, which indicate that fruit is in a suitable state for oviposition, are

available [96]. Honeybees are more likely to follow dances to find food, rather than search independently, when they are novice foragers than when experienced, but experienced foragers follow dances if their previous trip was unsuccessful [97]. Finally, as we have discussed, evidence that individuals use conspecific presence to identify unfamiliar food types, but ignore social information once experienced, can be found in honeybees, bumblebees, stingless bees and wasps.

Quantifying the Value of Social Information

To quantify the adaptive benefits of a behaviour pattern directly, one would ideally need a mutant that does not exhibit this pattern [14]. In some cases, however, it may be possible to disrupt information transfer by gentle methods, without otherwise affecting the animals' behaviour. Von Frisch's discovery of the honeybee dance language [31] represented one of the most exciting developments in the early history of behavioural ecology, but perhaps one of the most intriguing aspects of the dance is that so far, no equivalent referential system has been found in other social insects, despite similarities in life-history, social structure and cognitive abilities [30,45]. Is there something unusual about honeybee ecology which means that they, in particular, should benefit from learning socially about resource location?

Dancing honeybees indicate the direction of food with reference to the position of the sun, which is represented by the top of the vertical comb in the dark conditions of the hive. Thus, if hives are laid horizontally, dancers cannot communicate direction and orient themselves randomly [31,98] unless an artificial light source is present, which both dancers and recruits will use as an alternative reference point [31]. Surprisingly, when the food intake rate of colonies with and without the ability to communicate location is compared, it emerges that the information contained within the dance is valuable only under a narrow range of ecological conditions: during the Californian winter but not during spring or summer [99], and in the old world tropics but not in either warm or cold temperate European habitats [98].

Why should this be? It seems likely that the explanation reflects variation in the distribution of resources. In temperate winters, floral resources are patchily distributed and available for short periods of time [100], just as they are in the tropics [98], where the genus *Apis* originally diversified. If a forager is just as likely to find food by searching alone as by waiting for social information, communication should offer no advantage or may even impede fitness [87]. Thus, these studies provide a unique insight into the relationship between the adaptive benefits of social information use and ecology, paving the way for more detailed examination of the specific circumstances under which using social information increases biological competitiveness.

Concluding Remarks

Do honeybees indeed 'understand' how bumblebees manipulate flowers, as Darwin suggests? Probably not; the honeybees might have arrived at similar techniques by individual exploration, by using

bumblebees' scent cues or by a form of second order conditioning. Insects might tell us relatively little about the psychological processes behind imitation or about culture or social intelligence. Nonetheless, rather than simply providing a further addition to the long list of animals that use social information, the insects offer a unique perspective on the behavioural ecology of social learning — an opportunity to study the basic mechanisms of how social information enhances fitness through incorporation into everyday decisions, in an ecologically realistic setting. Perhaps the most valuable aspect, though, is that an insect perspective illustrates just how fundamental a role social learning can play in the lifestyle of any animal, even one whose brain is smaller than a grass-seed. Complex cognition may be a feature of some forms of social learning [38], but some of the most complex, self-organising societies function on the basis of very simple processes of information transfer between individuals.

One promising line of enquiry raised here is the manipulation of social information in order to assess its value in different ecological circumstances. Such manipulation is difficult to achieve when animals use inadvertent social information, but the tendency within social insect colonies to communicate about the environment via signalling lends itself to further development of this approach. Another question relates to the use of information provided by heterospecifics [17–19,101]. If heterospecifics utilise similar resources, or are eaten by similar predators, or share similar homes, learning from their behaviour may make evolutionary sense. On the other hand, perhaps social learning systems that are too flexible might lead to learning from inappropriate models, but so long as there is feedback via an evaluation of the success of copied behaviour patterns, this problem could be circumvented [42]. Alternatively, conspecific behaviour patterns might have higher default "credibility" in the view of the copying individual than the behaviour of heterospecifics, and this unlearned weighting might later be modified by experience. Finally, we also draw attention to the role of development in the ability to use social cues. Skinner [102] was the first to point out that animals may have ample opportunity in a natural environment to learn about whether to "copy" others or not, but the role of first or second-order conditioning in the establishment of social cue use remains a neglected area of research.

Our aim is to encourage further development of the exciting and promising experimental approaches highlighted here. Insects provide low-maintenance, versatile experimental models, easy to maintain in large numbers for high statistical power, and can be manipulated in the lab or field with minimal disturbance. If the study of social information use has, in previous years, sometimes failed to make full use of the invertebrate world, insect biologists have also failed to tie in their findings with the rich literature on vertebrate social learning. The studies that we describe above not only pave the way for more detailed examination of the full spectrum of social information types that insects may be found to make use of, but also illustrate that a combined approach may have much to offer both groups.

References

- Zentall, T., and Galef, B.J., eds. (1988). *Social Learning: Psychological and Biological Perspectives* (Hillsdale, New Jersey: Erlbaum).
- Heyes, C., and Galef, B.J., eds. (1996). *Social Learning and the Roots of Culture* (San Diego: Academic Press).
- Danchin, E., Giraldeau, L.A., Valone, T.J., and Wagner, R.H. (2004). Public information: from nosy neighbours to cultural evolution. *Science* 305, 487–491.
- Whiten, A., and Van Schaik, C.P. (2007). The evolution of animal “cultures” and social intelligence. *Phil. Trans. Roy. Soc. Lond. B.* 362, 603–620.
- Griffin, A.S. (2004). Social learning about predators: a review and prospectus. *Learning Behavior* 32, 131–140.
- Galef, B.G., and Laland, K.N. (2005). Social learning in animals: Empirical studies and theoretical models. *Bioscience* 55, 489–499.
- Giraldeau, L.A., and Caraco, T. (2000). *Social Foraging Theory* (Princeton: Princeton University Press).
- Romanes, G.J. (1884). *Mental Evolution in Animals* (New York: AMS Press).
- Darwin, C.R. (1841). Letter no. 607, from Charles Darwin to the Gardener’s Chronicle, published 21st August 1841. In *The Correspondence of Charles Darwin, Vol. 2* (Cambridge University Press 1986), pp. 1837–1843.
- Giurfa, M. (2003). The amazing mini-brain: lessons from a honey bee. *Bee World* 84, 5–18.
- Chittka, L., Dyer, A.G., Bock, F., and Dornhaus, A. (2003). Psychophysics: Bees trade off foraging speed for accuracy. *Nature* 424, 388.
- Giurfa, M., Zhang, S.W., Jenett, A., Menzel, R., and Srinivasan, M.V. (2001). The concepts of ‘sameness’ and ‘difference’ in an insect. *Nature* 410, 930–933.
- Menzel, R., Chittka, L., Eichmüller, S., Geiger, K., Peitsch, D., and Knoll, P. (1990). Dominance of celestial cues over landmarks disproves map-like orientation in honeybees. *Zeitschrift für Naturforsch* 45, 723–726.
- Raine, N.E., Ings, T.C., Dornhaus, A., Saleh, N., and Chittka, L. (2006). Adaptation, genetic drift, pleiotropy, and history in the evolution of bee foraging behavior. *Adv. Study Behav.* 36, 305–354.
- Chittka, L., Thomson, J.D., and Waser, N.M. (1999). Flower constancy, insect psychology, and plant evolution. *Naturwiss* 86, 361–377.
- Seeley, T.D. (1995). *The Wisdom of the Hive* (Cambridge, Massachusetts: Harvard University Press).
- Coolen, I., van Bergen, Y., Day, R.L., and Laland, K.N. (2003). Species difference in adaptive use of public information in sticklebacks. *Proc. Roy. Soc. Lond. B.* 270, 2413–2419.
- Rainey, H.J., Zuberbühler, K., and Slater, P.J.B. (2004). Hornbills can distinguish between primate alarm calls. *Proc. Roy. Soc. Lond. B.* 271, 755–759.
- Seyfarth, R., and Cheney, D. (1990). The assessment by vervet monkeys of their own and another species alarm calls. *Anim. Behav.* 40, 754–764.
- Laland, K.N. (2004). Social learning strategies. *Learning Behavior* 32, 4–14.
- Dall, S.R.X., Giraldeau, L.A., Olsson, O., McNamara, J.M., and Stephens, D.W. (2005). Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* 20, 187–193.
- Galef, B.J., and Giraldeau, L. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Anim. Behav.* 61, 3–15.
- Leadbeater, E., and Chittka, L. (2005). A new mode of information transfer in foraging bumblebees? *Curr. Biol.* 15, R447–R448.
- Kawaguchi, L.G., Ohashi, K., and Toquenaga, Y. (2006). Do bumble bees save time when choosing novel flowers by following conspecifics? *Functional Ecol.* 20, 239–244.
- Brian, A.D. (1957). Differences in the flowers visited by four species of bumble-bees and their causes. *J. Anim. Ecol.* 26, 71–98.
- Slaa, J.E., Wassenberg, J., and Biesmeijer, J.C. (2003). The use of field-based social information in eusocial foragers: local enhancement among nestmates and heterospecifics in stingless bees. *Ecol. Entomol.* 28, 369–371.
- Reid, B.L., Macdonald, J.F., and Ross, D.R. (1995). Foraging and Spatial-Dispersion in Protein Scavenging Workers of *Vespula germanica* and *V. maculifrons* (Hymenoptera, Vespidae). *J. Ins. Behav.* 8, 315–330.
- Richter, M.R., and Tisch, V.L. (1999). Resource choice of social wasps: influence of presence, size and species of resident wasps. *Ins. Soc.* 46, 131–136.
- Parrish, M.D., and Fowler, H.G. (1983). Contrasting foraging related behaviors in two sympatric wasps (*Vespula maculifrons* and *Vespula germanica*). *Ecol. Entomol.* 8, 185–190.
- Nieh, J.C. (2004). Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). *Apidol.* 35, 159–182.
- von Frisch, K. (1967). *The Dance Language and Orientation of Bees* (Cambridge, Massachusetts: Harvard University Press).
- Kevan, P., Giurfa, M., and Chittka, L. (1996). Why are there so many and so few white flowers? *Trends Plant Sci.* 1, 280–284.
- Chittka, L. (1997). Bee color vision is optimal for coding flower color, but flower colors are not optimal for being coded - Why? *Israel. J. Plant Sci.* 45, 115–127.
- Menzel, R. (1985). Learning in honey bees in an ecological and behavioral context. *Fortschritte der Zoologie* 31, 55–74.
- Menzel, R. (2001). Behavioral and neural mechanisms of learning and memory as determinants of flower constancy. In *Cognitive Ecology of Pollination: Animal Behaviour and Floral Evolution*, L. Chittka and J.D. Thomson, eds. (Cambridge: Cambridge University Press), pp. 21–40.
- Leadbeater, E., and Chittka, L. (2007). The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behav. Ecol. Sociobiol.* DOI: 10.1007/s00265-007-0412-4.
- Worden, B.D., and Papaj, D.R. (2005). Flower choice copying in bumblebees. *Biol. Lett.* 1, 504–507.
- Heyes, C. (1994). Social learning in animals: Categories and mechanisms. *Biol. Rev.* 69, 207–231.
- Bitterman, M.E., Menzel, R., Fietz, A., and Schäfer, S. (1983). Classical conditioning of proboscis extension in honeybees (*Apis mellifera*). *J. Comp. Psychol.* 97, 107–119.
- Dyer, A.G., Neumeyer, C., and Chittka, L. (2005). Honeybee (*Apis mellifera*) vision can discriminate between and recognise images of human faces. *J. Exp. Biol.* 208, 4709–4714.
- Galef, B.G., and Whiskin, E.E. (1997). Effects of social and asocial learning on longevity of food-preference traditions. *Anim. Behav.* 53, 1313–1322.
- Galef, B.J. (1995). Why behaviour patterns that animals learn socially are adaptive. *Anim. Behav.* 49, 1325–1334.
- Miller, N.E., and Dollard, J. (1941). *Social Learning and Imitation* (New Haven, Connecticut: Yale University Press).
- Fiorito, G., and Scotto, P. (1992). Observational learning in *Octopus vulgaris*. *Science* 256, 545–547.
- Dornhaus, A., and Chittka, L. (1999). Evolutionary origins of bee dances. *Nature* 401, 38.
- Galef, B.G., Mason, J.R., Preti, G., and Bean, N.J. (1988). Carbon disulfide - a semiochemical mediating socially-induced diet choice in rats. *Physiology Behavior* 42, 119–124.
- Gil, M., and De Marco, R.J. (2005). Olfactory learning by means of trophallaxis in *Apis mellifera*. *J. Exp. Biol.* 208, 671–680.
- Giurfa, M., and Nunez, J.A. (1992). Honeybees mark with scent and reject recently visited flowers. *Oecologia* 89, 113–117.
- Stout, J.C., Goulson, D., and Allen, J.A. (1998). Repellent scent-marking of flowers by a guild of foraging bumblebees (*Bombus* spp.). *Behav. Ecol. Sociobiol.* 43, 317–326.
- Goulson, D., Hawson, S.A., and Stout, J.C. (1998). Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species. *Anim. Behav.* 55, 199–206.
- Saleh, N., Scott, A.G., Bryning, G.P., and Chittka, L. (2007). Distinguishing signals and cues: Bumblebees use general footprints to generate adaptive behaviour at flowers and nest. *Arthropod-Plant Interactions* DOI: 10.1007/s11829-007-9011-6.
- Saleh, N., and Chittka, L. (2006). The importance of experience in the interpretation of conspecific chemical signals. *Behav. Ecol. Sociobiol.* 61, 215–220.
- Boyd, R., and Richerson, P. (1985). *Culture and the Evolutionary Process* (Chicago: University of Chicago Press).
- Saleh, N., Ohashi, K., Thomson, J.D., and Chittka, L. (2006). Facultative use of the repellent scent mark in foraging bumblebees: complex versus simple flowers. *Anim. Behav.* 71, 847–854.
- Gawleta, N., Zimmermann, Y., and Eitz, T. (2005). Repellent foraging scent recognition across bee families. *Apidologie* 36, 325–330.
- Reader, T., MacLeod, I., Elliott, P.T., Robinson, O.J., and Manica, A. (2005). Inter-order interactions between flower-visiting insects: Foraging bees avoid flowers previously visited by hoverflies. *J. Ins. Behav.* 18, 51–57.
- Nieh, J.C., Barreto, L.S., Contrera, F.A.L., and Imperatriz-Fonseca, V.L. (2004). Olfactory eavesdropping by a competitively foraging stingless bee, *Trigona spinipes*. *Proc. Roy. Soc. Lond. B.* 271, 1633–1640.
- Wisenden, B.D., Chivers, D.P., and Smith, R.J.F. (1997). Learned recognition of predation risk by *Enallagma damselfly* larvae

- (Odonata, Zygotera) on the basis of chemical cues. *J. Chem. Ecol.* 23, 137–151.
59. Cook, M., Mineka, S., Workenstein, B., and Laitsch, K. (1985). Observational conditioning of snake fear in rhesus monkeys. *J. Abnorm. Psychol.* 93, 355–372.
60. Galef, B.J. (1988). Imitation in animals: history, definitions and interpretation of the data from the psychological laboratory. In *Social Learning: Psychological and Biological Perspectives*, T. Zentall and B.J. Galef, eds. (Hillsdale, New Jersey: Erlbaum), pp. 3–28.
61. Coolen, I., Dangles, O., and Casas, J. (2005). Social learning in non-colonial insects? *Curr. Biol.* 15, 1931–1935.
62. Dawkins, R., and Krebs, J.R. (1978). Animal signals: Information or manipulation? In *Behavioural Ecology: An Evolutionary Approach*, J.R. Krebs and N.B. Davies, eds. (Sunderland, MA: Sinauer Associates), pp. 282–309.
63. Hölldobler, B., and Wilson, E.O. (1990). *The Ants* (Harvard University Press).
64. Free, J. (1957). The transmission of food between worker honeybees. *Brit. J. Anim. Behav.* 5, 41–47.
65. Farina, W.M., Gruter, C., and Diaz, P.C. (2005). Social learning of floral odours inside the honeybee hive. *Proc. Roy. Soc. B.* 272, 1923–1928.
66. Farina, W.M., Gruter, C., Acosta, L., and Mc Cabe, S. (2007). Honeybees learn floral odors while receiving nectar from foragers within the hive. *Naturwiss* 94, 55–60.
67. Caro, T.M., and Hauser, M.D. (1992). Is there teaching in nonhuman animals? *Quart. Rev. Biol.* 67, 151–174.
68. Franks, N.R., and Richardson, T. (2006). Teaching in tandem-running ants. *Nature* 439, 153.
69. Möglich, M., and Hölldobler, B. (1974). Social carrying behaviour and division of labor during nest moving in ants. *Psyche* 81, 219–236.
70. Pratt, S.C., Mallon, E.B., Sumpter, D.J.T., and Franks, N.R. (2002). Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax alpehennis*. *Behav. Ecol. Sociobiol.* 52, 117–127.
71. Leadbeater, E., Raine, N.E., and Chittka, L. (2006). Social learning: Ants and the meaning of teaching. *Curr. Biol.* 16, R323–R325.
72. Laland, K.N., Richerson, P., and Boyd, R. (1996). Developing a theory of animal social learning. In *Social learning in Animals: The Roots of Culture*, C.M. Heyes and B.G. Galef, eds. (San Diego, California: Academic Press Inc).
73. Hirata, S., Watanabe, K., and Kawai, M. (2002). “Sweet potato washing” revisited. In *Primate Origins of Human Cognition and Behaviour*, T. Matsuzawa, ed. (Tokyo: Springer).
74. Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. *Primates* 6, 1–30.
75. Marler, P. (1952). Variation in the song of the Chaffinch (*Fringilla coelebs*). *Ibis* 94, 458–472.
76. Donaldson, Z.R., and Grether, G.F. (2007). Tradition without social learning: a scent-based communal roost formation in a Neotropical harvestman (*Prionostemma* sp.). *Behav. Ecol. Sociobiol.* 61, 801–809.
77. Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature* 437, 52–55.
78. Galef, B.G. (1992). The question of animal culture. *Human Nature* 3, 157–178.
79. Gandolfi, M., Mattiacci, L., and Dorn, S. (2003). Preimaginal learning determines adult response to chemical stimuli in a parasitic wasp. *Proc. Roy. Soc. Lond. B.* 270, 2623–2629.
80. Ray, S. (1999). Survival of olfactory memory through metamorphosis in the fly *Musca domestica*. *Neurosci. Lett.* 259, 37–40.
81. Hopkins, A.D. (1917). A discussion of C.G. Hewitt’s paper on “Insect Behavior”. *J. Econ. Entomol.* 10, 92–93.
82. Lindauer, M. (1985). The dance language of honeybees: The history of a discovery. In *The Dance Language of Honeybees: The History of a Discovery*, B. Hölldobler and M. Lindauer, eds. (Sunderland, MA: Sinauer), pp. 129–140.
83. Kirchner, W.H. (1987). Tradition im Bienenstaat: Kommunikation zwischen den Imagines und der Brut der Honigbiene durch Vibrationssignale. PhD dissertation, Julius-Maximilians Universität, Würzburg.
84. Seeley, T.D. (1978). Life history strategy of the honey bee, *Apis mellifera*. *Oecologia* V32, 109–118.
85. Boyd, R., and Richerson, P. (1988). An evolutionary model of social learning: the effects of spatial and temporal variation. In *Social Learning: Psychological and Biological Perspectives*, T.R. Zentall and B.G. Galef, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates), pp. 29–48.
86. Giraldeau, L.A., and Beauchamp, G. (1999). Food exploitation: searching for the optimal joining policy. *Trends Ecol. Evol.* 14, 102–106.
87. Dechaume-Moncharmont, F.X., Dornhaus, A., Houston, A.I., McNamara, J.M., Collins, E.J., and Franks, N.R. (2005). The hidden cost of information in collective foraging. *Proc. Roy. Soc. Lond. B.* 272, 1689–1695.
88. Franks, N.R., Pratt, S.C., Mallon, E.B., Britton, N.F., and Sumpter, D.J.T. (2002). Information flow, opinion polling and collective intelligence in house-hunting social insects. *Phil. Trans. Roy. Soc. B.* 357, 1567–1583.
89. Seeley, T.D., and Visscher, P.K. (2004). Group decision making in nest-site selection by honey bees. *Apidologie* 35, 101–116.
90. Lindauer, M. (1955). Schwarmbienen auf Wohnungssuche. *Z. Vergl. Physiol.* 37, 263–324.
91. Seeley, T. (1985). *Honeybee Ecology* (Princeton, New Jersey: Princeton University Press).
92. Seeley, T.D., and Buhrman, S.C. (2001). Nest-site selection in honey bees: how well do swarms implement the “best-of-N” decision rule? *Behav. Ecol. Sociobiol.* 49, 416–427.
93. Visscher, P.K., and Camazine, S. (1999). Collective decisions and cognition in bees. *Nature* 397, 400.
94. Giraldeau, L.A., Valone, T.J., and Templeton, J.J. (2002). Potential disadvantages of using socially acquired information. *Phil. Trans. Roy. Soc. Lond. B.* 357, 1559–1566.
95. Kendal, R.L., Coolen, I., van Bergen, Y., and Laland, K.N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Adv. Study Behav.* 35, 333–379.
96. Prokopy, R.J., and Roitberg, B. (2001). Joining and avoidance behaviour in nonsocial insects. *Ann. Rev. Entomol.* 46, 631–665.
97. Biesmeijer, J., and Seeley, T. (2005). The use of waggle dance information by honey bees throughout their foraging careers. *Behav. Ecol. Sociobiol.* 59, 133–142.
98. Dornhaus, A., and Chittka, L. (2004). Why do honey bees dance? *Behav. Ecol. Sociobiol.* 55, 395–401.
99. Sherman, G., and Visscher, P.K. (2002). Honeybee colonies achieve fitness through dancing. *Nature* 419, 920–922.
100. Visscher, P.K., and Seeley, T.D. (1982). Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63, 1790–1801.
101. Chittka, L., and Leadbeater, E. (2005). Social learning: Public information in insects. *Curr. Biol.* 15, R869–R871.
102. Skinner, B.F. (1953). *Science and Human Behaviour* (New York: Free Press).
103. Chittka, L. (2004). Dances as windows into insect perception. *PLoS Biol.* 2(7), e216.
104. Seeley, T.D., and Buhrman, S.C. (1999). Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* 45, 19–31.