

SOCIAL INFORMATION USE IN SOCIAL INSECTS

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Statement of Originality

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Details of collaboration and publications:

Chapter 2: The experimental protocol was designed by Dr Elli Leadbeater, Dr Aurore Avargues-Weber and me. Data was also collected by the aforementioned, with assistance from Charlotte Lockwood and Adam Devenish.

Chapter 4: I designed the experiment with help from Dr Johannes Spaethe at the University of Wurzburg. I conducted experiments with field assistance from Lowri Watkins.

Chapter 5: Dr Elli Leadbeater and I designed the experiment and I collected the data.

Publications arising from this thesis

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Dawson, E. H. & Chittka, L. 2014. Bumblebees (*Bombus terrestris*) use social information as an indicator of safety in dangerous environments. *Proceedings of the Royal Society B* **281**, 20133174.

Review article

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Abstract

Social learning plays a valuable role in the lives of many animal taxa, sometimes allowing individuals to bypass the costs of personal exploration. The ubiquity of this behaviour may arise from the fact that learning from others is often underpinned by simple learning processes that also enable individuals to learn asocially. Insects have proven to be particularly valuable models for investigating parsimonious hypotheses with regards to social learning processes, due to their small brain sizes and the prevalence of social information use in their life histories. In this thesis, I use social insects to further investigate the mechanisms underlying more complex social learning behaviours and explore the circumstances under which social information use manifests.

In the first chapter, I investigate the proximate mechanisms underlying social learning and demonstrate that even seemingly complex social learning behaviours can arise through simple associative learning processes. In Chapter two, I investigate whether bees are more predisposed to learning from conspecific cues and discover that social information is learnt to a greater extent than information originating from non-social sources. In Chapter four, I demonstrate that classical conditioning also underpins learning from evolved social signals in honeybees. Finally, I investigate whether social information is used adaptively by bumblebees: Chapter three demonstrates that joining behaviour in free-flying bees is contingent upon whether flowers are familiar or not, and in Chapter six, I show that when social information is costly to acquire, bees are more likely to rely on social information to make foraging decisions.

Taken as a whole, my findings suggest that bees may be specially adapted for receiving social information, but the ability to learn from others arises through general associative learning mechanisms.

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Chapter 1: Introduction

1.1 The mechanisms underlying social learning and social information use

1.1.1 The evolution of social learning abilities

The ability to learn from others is a fundamental feature of human societies, facilitating the spread of fitness enhancing behaviours and enabling us to adapt to, and inhabit, all corners of the Earth (Boyd et al., 2011). This remarkable feat arises, not through specialised physical adaptations, but through the accretion of knowledge passed from generation to generation, also known as culture (Whiten et al., 1999). Yet, learning from others is not solely confined to humans; an extremely rich diversity of animal taxonomies is known to factor information derived from other individuals in their decision making processes.

Social learning is broadly defined as ‘...learning that is facilitated by observation of, or interaction, with another individual (or its products)’ (Heyes, 1994; Hoppitt and Laland, 2013), a definition which encompasses many remarkable behavioural feats observed in the animal kingdom. Almost all animals interact with conspecifics through evolved signals or communicatory systems, yet, typically, research in the field of social learning, instead, focuses on the use of social cues made available *inadvertently* by other individuals (Heyes, 1994; Hoppitt and Laland, 2008; Heyes, 2012). Using such coincidental social information, animals have the opportunity to

learn about optimal places to feed, whom to mate with, what predators to avoid and where to establish a home without incurring the costs of individual exploration (Galef Jr and Giraldeau, 2001; Griffin, 2004; Seppänen and Forsman, 2007; Mery et al., 2009).

Most animals are capable of learning individually, enabling them to modify their behaviour to their environment through experience (Shettleworth, 1998). It has long been assumed that the learning mechanisms which underpin individual learning are cognitively distinct from those which mediate social learning processes and that social learning abilities are specialised adaptations which arose through selection pressures from living in a social environment (Klopfer, 1959, 1961; Templeton et al., 1999). Yet, recent debate has questioned whether social and asocial learning are, in fact, cognitively distinct processes (Heyes, 1994, 2012).

Firstly, social learning processes are ubiquitous, occurring in a wide variety of unrelated species, suggesting that the mechanisms that underlie such learning are also taxonomically common (Heyes, 2012).

Secondly, social learning abilities appear not to be restricted to group-living animals; solitary species such as the octopus (*Octopus vulgaris*) and red-footed turtle (*Geochelone carbonaria*) also demonstrate the ability to learn from others (Fiorito and Scotto, 1992; Wilkinson et al., 2010). These findings contradict the hypothesis that social learning abilities arose to facilitate living in groups and once again suggest that the underlying social learning mechanisms are not cognitively specialised (Heyes, 2012).

Finally, there is considerable evidence that within a number of different species, social and individual learning abilities are correlated (Lefebvre et al., 1996; Reader and Laland, 2002; Reader, 2003; Bouchard et al., 2007; Boogert et al., 2008). For example, blue tits (*Cyanistes caeruleus*) that are particularly good at independently solving a novel foraging task, also show strong social learning abilities (Aplin et al., 2013). These findings suggest that the learning mechanisms that mediate learning from others are the same as those that enable an animal to learn individually (Heyes, 2012).

1.1.2 Classical conditioning leads to social learning

Based on this evidence, Heyes (1994, 2012) suggested that these common learning processes are associative mechanisms which enable an animal to form predictive relationships between environmental contingencies. Associative learning occurs universally in an extremely extensive range of animal taxonomies, from humans to nematodes (Nuttley et al., 2002; Miller and Shettleworth, 2007), and underlies many of the behaviours in an animal's repertoire, such as navigation (Miller and Shettleworth, 2007), predator avoidance (Griffin, 2004), and enhancing biological fitness (Adkins-Regan and MacKillop, 2003). For example, it was found that a higher number of fertilized eggs would be produced when male and female Japanese quail (*Coturnix japonica*) were placed in a cage that had previously been associated with the presence of a mate than when kept in cages that had no such association (Adkins-Regan and MacKillop, 2003).

Researchers have attempted to classify social learning processes into distinct psychological processes, all of which can be explained by associative mechanisms akin to those underlying asocial learning. The most straightforward of these processes is where observation of another individual exposes the learner to a stimulus or location resulting in an increased interaction with that stimulus type (known as stimulus enhancement) or specific location (known as local enhancement) (Heyes, 1994; Hoppitt and Laland, 2008). For example, rats (*Rattus norvegicus*) observing a conspecific pulling down a lever to obtain food were much faster in acquiring this behaviour themselves than control individuals who had not observed demonstrators (Jacoby and Dawson, 1969). If the rats were attracted to scent-marks deposited on the lever by the demonstrator rat, this would be classified as local enhancement, but if the sight of a demonstrator pulling the lever resulted in the observer concentrating its attentions on the lever, this would be categorised as stimulus enhancement (Heyes et al., 2000). While classified under the umbrella of social learning, these processes do not involve direct social learning (Hoppitt and Laland, 2013). Rather, the socially mediated exposure to a stimulus, or ‘social information’, may result in subsequent individual learning through classical conditioning. For example, an observer rat may simply be attracted towards the lever as a result of a social presence, but consequent individual learning may then occur if the rat obtains food and subsequently associates the lever with food.

Another type of social learning process is observational conditioning which was originally conceived with associative learning in mind and fits within a Pavlovian framework. In this process, a social stimulus provokes an individual to produce an unconditioned response. If another neutral stimulus is present at the same time, it

becomes associated with the social stimulus through simple Pavlovian conditioning. Consequently, this previously neutral stimulus will now trigger an unconditioned response in the learner, even in absence of the social stimulus (Cook et al., 1985; Heyes, 1994; Shettleworth, 1998; Hoppitt and Laland, 2008). A classic example derives from the bird literature, specifically mobbing behaviour in blackbirds (*Turdus merula*). These birds, on detection of a predator, will approach in a group and mob the potential predator, alerting others to the threat and driving away the predator (Cully and Ligon, 1976; Curio et al., 1978). Curio and colleagues (1978) discovered that through social transmission, a naïve bird can learn to mob a previously unfamiliar predator. If the inexperienced bird hears and sees a conspecific mobbing a harmless object, such as a honeyeater or a plastic bottle, the bird will later mob that object, even in absence of other birds, through simple Pavlovian conditioning (Curio et al., 1978; Shettleworth, 1998). Once again, exposure to the social stimulus subsequently results in learning for the observer. In this thesis I will investigate a similar behaviour in honeybees, by exploring whether bees can socially acquire predator avoidance behaviour through classical conditioning.

Even imitation - the act of performing the same motor action as a demonstrator - a seemingly complex social learning process, can be placed in an associative framework (Catmur et al., 2009; Cook et al., 2014). Imitation lies at the other end of the social learning spectrum, where it has been hotly debated as the most cognitively challenging form of social learning, which is restricted to humans (Thorndike, 1911). Yet, recent research highlights that imitation occurs in both human and non-human animals (Akins and Zentall, 1998; Saggerson et al., 2005; Range et al., 2011), and that at first glance, what appears to a complicated and sophisticated behaviour, may

in fact be significantly simpler than originally thought (Heyes, 2011). In general, imitation results in an animal copying the motor pattern, or movements, of a conspecific so that the pattern can be replicated independently (Heyes, 1994). In some cases, an animal will simply reproduce the results of an observed behaviour without performing the movement with true fidelity, a process often referred to as emulation (Huber et al., 2009). For example, chimpanzees (*Pan troglodytes*) observing conspecifics using a tool, in one of two ways, to obtain food, were also subsequently able to retrieve the food but without implementing the tool in precisely the same way that was observed (Tomasello et al., 1987). Associative learning may account for such processes if, for example, the chimpanzee simply associates the observed tool with food, resulting in an increased interaction with that tool (Huber et al., 2009).

In contrast, more complex forms of imitation require that an animal not only imitates motor movements precisely, but that intentionality underlies the imitation in order to reach a direct goal (Thorndike, 1911). For example, Japanese quail that observed demonstrators either pecking or stepping on a treadle, were more likely to imitate a specific action if they saw demonstrators receive a food reward after performing that action (Akins and Zentall, 1998). It is more difficult to view such cases from an associative learning perspective since the animal is required to form a correspondence between a visual representation of an action and its own motor response to that action (Heyes, 2001; Brass and Heyes, 2005). Mirror neurons, discovered in monkeys 20 years ago, have been implicated in the facilitation of imitation (Iacoboni et al., 1999) due to the remarkable feature that they not only fire when an individual performs an action, but also respond when the individual

observes another animal performing the same action (Pellegrino et al., 1992). Recently, it has been proposed that these specialised neuronal responses arise, not through genetic adaptations, but through associative learning processes (Catmur et al., 2009; Cook et al., 2014). It is suggested that through experience of seeing and doing an action simultaneously, a connection is established between the sensory and motor neurons, strengthened through associative learning (Cook et al., 2014). Therefore, on subsequent observation of a similar action performed by another agent, these motor neurons, now transformed into mirror neurons, will fire.

Although these social learning processes can be encompassed within an associative, and therefore, individual learning framework, there is still an implicit assumption that animals are adapted to treat conspecific behaviour as a biologically relevant stimulus. For example, in the case of local enhancement, an animal is exposed to a stimulus through its *attraction* towards a conspecific, or its products, and only subsequently does associative learning then occur. So are animals specially adapted to respond to conspecific information or could they also learn the value of this behaviour through individual learning? For example, an animal may be drawn to, or, equally, avoid conspecifics as a result of previous positive or negative contingencies experienced with social cues (Heyes, 1994; Saleh and Chittka, 2006; Leadbeater and Chittka, 2009). In Chapter two, I will explore this question by assessing whether learning by observation arises through associations with conspecifics.

1.2 Social information use in social insects

1.2.1 Social insects as a model for studying social learning

Eusocial bees live in nests which often consist of 100s to 1000s of highly related individuals, a high proportion of which (e.g. larvae) cannot search for their own food and are entirely dependent on other members of the colony. In order to sustain such large numbers of nest members there are enormous selection pressures on the efficient collection of food which is essential for the survival of a colony. Yet these bees often forage in highly unpredictable environments where the choices of available flowers are vast and ephemeral; nectar and pollen resources change enormously in quality and availability, not just on a seasonal level, but also multiple times a day (Pleasants and Zimmerman, 1979; Biernaskie and Cartar, 2004; Herrera et al., 2006). Therefore, considerable effort must be expended to find and keep track of the most profitable resources (Heinrich, 1979). In order to keep abreast of their fluctuating environments, bees rely on a number of strategies in order to maximise their foraging efforts. Firstly, an unexperienced forager can resort to innate, unlearned floral preferences such as floral shape (Rodríguez et al., 2004) and colour (Giurfa et al., 1995; Raine and Chittka, 2007). Alternatively, a forager can learn about the relative profitability of different flower types through personal sampling of their environment. By experiencing a rewarding or recently depleted flower, bees can quickly learn a wide range of associated floral characteristics such as colour (Heinrich et al., 1977), odour (Wright and Schiestl, 2009) and symmetry (Giurfa et al., 1996) which could assist them in future foraging trips.

Social environments, such as those found in eusocial colonies, offer an optimal background for the manifestation of social learning processes, clearly demonstrable by the many different social cues which are thought to have, through time, evolved into signals in bees, ants and wasps (Tinbergen, 1952; Coussi-Korbel and Frigaszy, 1995; Grüter and Leadbeater, 2014). Yet, social insects can also learn about biologically important information by simply making use of information provided coincidentally by other individuals. While bees are typically independent foragers (although social signalling of food locations does occur in honeybees and some species of stingless bee), they nonetheless share their environment with other individuals who feed from the same flowers and face the same foraging challenges, offering abundant opportunities for socially acquiring relevant foraging information (Waser, 1982; Waser et al., 1996; Leadbeater and Chittka, 2007b).

Traditionally, concurrent foraging between pollinators has been viewed in light of competition for resources (Inouye, 1978; Thomson et al., 1987; Sandlin, 2000), yet recent research has highlighted that bees and other social insects are able to use social cues originating from conspecifics to identify which flowers to visit (Goulson et al., 1998; Stout and Goulson, 2001; Leadbeater and Chittka, 2005; Worden and Papaj, 2005; Leadbeater and Chittka, 2007a, b, 2008, 2009; Goulson et al., 2013; Mirwan and Kevan, 2013; Plowright et al., 2013; Leadbeater and Florent, 2014). Furthermore, social insects have proven to be a very valuable model system for understanding social learning processes since their foraging experience and environment can be strictly controlled in the laboratory, making it possible to delve into the mechanisms behind social learning behaviours, as well as investigating the

circumstances in which learning from others might arise (Leadbeater and Chittka, 2007b; Grüter and Leadbeater, 2014).

1.2.2 Learning to use social signals

Perhaps the most well-known and studied examples of social learning in the bee literature is the dance language performed by honeybees. Upon returning to the nest, a forager or ‘scout’ will communicate the location of a profitable food source, or potential nesting site, by performing a figure of eight waggle dance, which communicates distance and direction to nestmates (von Frisch, 1967). Although typically considered to be an evolved stereotyped behaviour, there is evidence that bees show a degree of flexibility when decoding nestmate dances (Su et al., 2008). Two different species of honeybee, *Apis mellifera* and *Apis cerana* are found to have distinct dance dialects, differing in the duration of waggle runs. Yet, when cross-fostered to the same hive, *A. cerana* is able to decipher the waggle dance of *A. mellifera* (Su et al., 2008) suggesting that some fine-tuning of the interpretation of dances occurs, at least in part, through individual learning processes. Foreign workers, on first encounter with the new dance dialect, must arrive at non-rewarding locations and, as a result, on subsequent journeys, must re-tune their decoding of the dance in order to reach the communicated food source (Avarguès-Weber et al., 2013).

Associative learning also plays an important role within the honeybee nest. Foragers will often engage in a trophallactic interaction upon returning to the hive, whereby a receiver bee will insert her proboscis into the forager’s mouth and sample a small

volume of recently collected nectar (von Frisch, 1967). Studies have shown that through this social food transfer, receiver bees associate the odour of nectar with food, enabling them, on subsequent foraging trips, to identify profitable flowers based on floral odours alone (Gil and De Marco, 2005). Information about profitable flower odours is also transmitted within bumblebee nests (Dornhaus and Chittka, 1999). Upon their return, successful foragers will perform excited runs around the nest, sharing the scents of rewarding flowers and distributing a pheromone which motivates inactive foragers into seeking these new food bounties (Dornhaus and Chittka, 1999; Dornhaus and Chittka, 2001; Dornhaus et al., 2003; Granero et al., 2005).

These communicatory signals also extend outside the nest. Some species of stingless bee and ant deposit scent trails leading to rewarding food sources, facilitating the recruitment of nestmates (Tumlinson et al., 1972; Hrncir et al., 2004; Jarau et al., 2004; Schorkopf et al., 2007). Typically these pheromonal deposits are species specific, suggesting individuals are innately predisposed to respond to such signals, yet, recent evidence suggests that individual learning modifies, to a degree, the way social signals are used. The stingless bee species, *Scaptotrigona pectoralis*, follows scent-trails originating from nest members, but generally ignores those deposited by other conspecific nests (Jarau, 2009). Yet, if foreign conspecific trail pheromones are included in the nest of *S. pectoralis*, before any foraging has taken place, workers are significantly more likely to use these foreign trails, suggesting that recognition of trail pheromones is a flexible behaviour that arises, in part, through learning (Reichle et al., 2011).

1.2.3. Learning to use inadvertent social cues

Social learning in insects has traditionally been discussed in light of these evolved signals, yet, there is also considerable evidence that insects also respond to, and use, information produced inadvertently by other individuals. By using social cues, bees and other pollinators can improve their foraging efficiency. For example, bumblebees produce tarsal cuticular hydrocarbons which are thought to reduce desiccation and improve adhesion to surfaces (Jiao et al., 2000; Eltz, 2006). These ‘footprints’, inadvertently left on flower surfaces, are repelling to future visitors, presumably because they indicate the flower has recently been depleted of its floral rewards (Goulson et al., 1998; Williams, 1998; Stout and Goulson, 2001; Reader et al., 2005). Yet, this avoidance response is not genetically predetermined; naïve bees, with no prior foraging experience, ignore these footprints (Leadbeater and Chittka, 2011), and if scent marks predict floral rewards, as opposed to a depleted flower, bees are, instead, attracted to these tarsal secretions (Saleh and Chittka, 2006).

The sight of other foragers at a resource can also be adaptively exploited when making foraging decisions. A wide array of pollinating insects, such as honeybees, wasps and stingless bees readily join conspecifics already feeding at flowers (local enhancement), potentially enabling them to locate feeding areas (Raveret Richter and Tisch, 1999; D’adamo et al., 2003; Slaa et al., 2003; Leadbeater and Chittka, 2005; Kawaguchi et al., 2006; Otis et al., 2006; Kawaguchi et al., 2007; Leadbeater and Chittka, 2007a). Again, joining responses most likely reflect prior associations experienced with conspecifics. Leadbeater and Chittka (2009) demonstrated that bumblebees will only preferentially join conspecifics on artificial flowers if previous

experience led them to associate conspecifics with sucrose; without this reliable association, bees join conspecifics at random.

It is clear to see how classical conditioning could give rise to the use of social cues, but could a similar mechanistic explanation be applied to the social transmission of novel foraging techniques? Many bees carry out ‘nectar robbing’, whereby small holes are made at the base of a flower’s corolla, allowing the bee to extract nectar without pollinating the flower (Inouye, 1983). Darwin first suggested that the spread of this behaviour may arise through social learning (Darwin, 1841), with more recent evidence demonstrating that bumblebees socially copy which side of the flower to bite through (Goulson et al., 2013). While such a phenomenon might suggest a more complex cognitive underlying behavioural mechanism (Darwin invoked an ‘imitation’ process), it was shown that this nectar-robbing behaviour can simply arise through interaction with the products of conspecific behaviour (Leadbeater and Chittka, 2008). Bumblebees were more likely to become nectar robbers themselves if they fed from holes created by previous robbers, presumably due to an association made between food and the base of the corolla, resulting in an increased interaction with that part of the plant (Leadbeater and Chittka, 2008). It is also possible, that through attraction towards conspecifics (also arising through associative learning), bees might discover these created holes more readily.

In addition to foraging behaviour, social information use has also been shown to play an important role in the avoidance of predators. Pollinators are the targets of many different types of predators, such as web building spiders, or those that sit and wait on flowers for unsuspecting prey, as well as a whole range of hymenoptera, diptera and birds (Dukas, 2001b). Personal learning can play an important role in avoiding

these predators. For example, since the majority of predator attempts on bees are unsuccessful (Morse, 1979, 1981, 1986), individuals are quickly able to learn and avoid floral patches that might harbour predators (Ings and Chittka, 2008, 2009). Yet, there is a high degree of risk associated with individually learning to avoid predators, and in such a scenario, using information provided by others may offer a safer strategy.

Previously, research on anti-predator behaviour in social insects has focussed on chemical signals which alert nestmates to predator threats at the hive (Jeanne, 1981; Breed et al., 2004). More recently it was also discovered that even away from the nest, bees can use social cues to avoid landing on flowers potentially concealing predators. For example, honeybees who encountered an attack at a food source will return to the nest and relay stop signals to nestmates to prevent them from visiting the same dangerous location (Nieh, 2010). Bees can also use cues that are (potentially) emitted inadvertently by other individuals. The presence of dead honeybees on flowers repels conspecifics from also landing (Dukas, 2001a), and both bumblebees and honeybees avoid areas associated with conspecific haemolymph, a likely cue of predation (Goodale and Nieh, 2012). While these cues may be shaped by selection to signal to conspecifics within the nest, it is also possible that bees learn the value of these social cues through associations; if haemolymph, or other conspecific alarm products, are experienced in conjunction with a failed personal attack, bees may subsequently use these cues as a predictor of predator presence.

Since associative learning mechanisms mediate the use of inadvertent social information, social cues should be viewed as another type of environmental cue that

can be used to predict environmental contingencies. From this perspective animals should also be expected to glean fundamental information from members of other species in the same environment (Avarguès-Weber et al., 2013). Indeed, there are now a considerable number of documented cases of social learning across species boundaries in insects and other animals. For example, as well as avoiding the haemolymph of conspecifics, bumblebees are also deterred by haemolymph emitted from heterospecific honeybees (Goodale and Nieh, 2012). Many different species of social insects feed concurrently in the same environment, and are hunted by the same predators, creating plenty of opportunity for using inadvertent information provided by heterospecific species. Yet, do animals learn all cues that are simply reinforced by reward or punishment or are they more predisposed to learning information originating from their own species? After all, the needs of conspecifics will fully reflect those of the learner, perhaps providing a more pertinent model to learn from. In Chapter three, I investigate this question by assessing whether bumblebees form stronger associations with conspecifics than with heterospecific provided information.

1.2.4 Using social information adaptively

The use of social information is typically discussed in light of its advantages because individuals can bypass the energy costs and predation risks that are associated with individual exploration. Yet, solely relying on social information to make decisions is an intrinsically maladaptive strategy; if the majority of individuals are dependent upon social sources, then the likelihood of copying outdated or incorrect information

increases considerably, leading to suboptimal choices (Giraldeau et al., 2002; Laland, 2004; Rieucou and Giraldeau, 2011). Furthermore, exclusively copying others may lead to higher levels of competition amongst individuals, resulting in overexploitation of resources and other potentially negative consequences such as increased attraction of predators or intraspecific aggressive interactions (Seppänen et al., 2007; Avarguès-Weber et al., 2013). Animals should therefore be discerning when choosing to use social information (Giraldeau et al., 2002; Laland, 2004). Consequently, it is suggested that animals may adopt ‘social learning strategies’ – either through genetically predetermined responses or by learning about the costs and benefits of copying – which enables individuals to use social information in an adaptive manner (Laland, 2004; Rendell et al., 2010; Grüter and Leadbeater, 2014).

One possible social learning strategy might involve selectively choosing who to copy from (Laland, 2004). There is considerable evidence in the social learning literature that suggests that animals will preferentially choose to copy a behaviour based on the number of individuals performing it (also known as conformity; (Henrich and Boyd, 1998; Lachlan et al., 1998; Day et al., 2001; Laland, 2004; Morgan et al., 2012)). For example, in humans, the likelihood of copying increases non-linearly with the number of demonstrators (Morgan et al., 2012) and in the insect world, ants are more likely to disproportionately follow a trail which has a higher concentration of pheromone deposits (Detrain and Deneubourg, 2008). Conforming to the most popular behaviour may have the highest payoff if the number of individuals denotes the success of a behaviour (Grüter and Leadbeater, 2014).

Many species have also been shown to resort to using social information when personal information is costly to acquire (Templeton and Giraldeau, 1996; Laland,

2004). For example, bumblebees are more likely to use conspecific footprints if they are found on flowers that require time consuming, complex handling as opposed to flowers which are relatively simple to feed from (Saleh et al., 2006). Bumblebees also show conditional attraction towards conspecifics; when foraging on new flower types, individuals are more likely to join conspecifics, bypassing the costs and risks of trial and error individual learning, yet, when presented with familiar flowers, conspecifics are ignored (Leadbeater and Chittka, 2005; Kawaguchi et al., 2007). Additionally, honeybees trained to feeders placed 1000m away from the hive followed nestmate waggle dances more frequently than when trained to feeders positioned 100m away (Wray et al., 2012). In Chapter six, I further investigate whether bumblebees adaptively use social information, by exploring the effect of predation risk on using personal and social information.

1.3 Structure of thesis

The aim of this thesis is to further understand the mechanisms which make using information from others possible, as well as exploring some of the circumstances in which social information use arises in bees.

Chapter 2: Learning by observing others emerges through associations

Associative learning plays a critical role in the development of learning from others, yet, this explanation is not so easily extended to more complex social learning phenomena. In this chapter, I show that learning by observation, a seemingly

complicated behaviour, can emerge through a simple series of associations, known as second-order conditioning, in bees.

Chapter 3: Conspecific and heterospecific information use in bumblebees

In this chapter, I explore whether bumblebees are specially adapted for learning information from conspecific sources or whether associations can be made freely across the species boundary. I compare learning performances between bees trained to associate conspecifics, heterospecific honeybees and non-social cues with rewarding food.

Chapter 4: A field exploration of social information use in bumblebees

Social learning has been extensively studied in laboratory settings where there is a strict control of variables. Yet these conditions are not entirely representative of those found in the wild, rendering the ecological validity of such findings as questionable. In this chapter, I investigate to what degree social information plays a role in the foraging decisions of free-flying bees in their natural environment.

Chapter 5: Socially acquired predator recognition in honeybees

The final part of this thesis investigates another facet of social learning; predator avoidance. In this chapter, I explore the learning mechanisms which give rise to socially acquired predator avoidance behaviour in honeybees.

Chapter 6: Using social information to locate safe foraging patches

Bees are known to use conspecific alarm products to avoid predators, yet simply joining undisturbed conspecifics could also result in a safe foraging option. In this chapter, I explore whether bees use social information conditionally and find that individuals show an increased attraction to nestmates when foraging in a dangerous versus safe environment.

Chapter 7: General discussion and conclusions

In the final chapter, I bring together my findings to readdress the question of whether social learning emerges through specialised adaptations or simply occurs as a result of individual learning abilities.

Chapter 2: Learning by observing others emerges through associations

Data from this chapter are published as:

Dawson, E.H., Avarguès-Weber, A., Chittka, L. & Leadbeater, E. 2013. Learning by observation emerges through simple associations in an insect model. *Current Biology*, **23**, 1-4.

2.1 Abstract

Associative learning plays a crucial role in the development of social learning processes, whereby an individual can form simple associations between social cues and the presence of food, predators or optimal habitats. However, more complex facets of social learning do not involve such obvious or direct associations, suggesting that more specialised cognitive mechanisms may be at play. Here we provide evidence to the contrary, by demonstrating that learning by observing others, a seemingly complex social learning phenomenon, arises through a series of simple associations, a process known as second-order conditioning. Bumblebees that watch other bees choosing a particular flower colour will later preferentially visit that colour when allowed to select their own flowers. We found that previous associations made with conspecifics were integral to this behaviour. Bees previously trained to associate conspecifics with rewarding food copied flower colours, while those without this training did not. Furthermore, we found that bees that had associated demonstrators with an aversive stimulus, actively avoided the flower colour they had previously seen conspecifics foraging from. Our findings offer a

parsimonious mechanistic explanation for a seemingly complex social learning phenomenon, which requires only the ability to integrate two or more learnt associations.

2.2 Introduction

It has long been assumed that an animal's ability to learn from others arises from specialised cognitive adaptations which facilitate living in social groups (Klopfer, 1961; Templeton et al., 1999). From this perspective, the mechanisms which mediate social learning have evolved independently and are completely distinct from those which enable animals to learn individually (Heyes, 2012). Yet, more recently this hypothesis has been challenged, with emerging evidence suggesting that social and individual learning abilities are derived from the same learning mechanisms; associative processes which enable an animal to form excitatory or inhibitory relationships between stimuli (Heyes, 1994, 2012). From this viewpoint, social information is just another type of environmental cue that can be used to predict relationships (Chittka and Leadbeater, 2005; Leadbeater and Chittka, 2007b), and therefore any animal capable of associative learning could potentially learn socially (Heyes, 2012). For example, through associative learning, bees can use the presence of conspecifics on flowers to identify profitable food patches by experiencing both the presence of bees and rewarding nectar simultaneously (Leadbeater and Chittka, 2005, 2009). Simply learning to associate conspecific behaviour with feeding areas, food types or predation risk might account for many instances of social learning found in the literature. Yet, more complex forms of social learning, such as

‘observational conditioning’, do not necessarily involve such obvious or direct associative relationships and hint at more specialised cognitive adaptations.

Observational conditioning occurs when an animal learns about a relationship between two stimuli through the observation of another animal’s behaviour (Heyes, 1994; Hoppitt and Laland, 2008). A classic example derives from the primate literature, where Mineka et al. (1984) demonstrated that baby rhesus macaques (*Macaca mulatta*), born and reared in the lab, display a fear response towards snakes only after they have observed adults responding fearfully to the snakes (Cook et al., 1985). This fear acquisition is mediated, to a degree, by associative learning, whereby the sight of a fearful conspecific triggers an unconditioned fear response in the babies, which subsequently becomes conditioned to the snake, simply by being observed in parallel (Cook et al., 1985). However, in order for this observational conditioning to occur, there is still an implicit assumption that an animal must possess a ‘pre-programmed’ response to a social stimulus, in this case an innate fear response induced by a frightened conspecific.

In this chapter, we explore an alternative hypothesis that learning by observing others might not, in all cases, be dependent upon an unconditioned, innate response to social behaviour, but instead arises through a series of associative processes (Heyes, 1994). For example, the baby monkey might first *learn* to associate fearful conspecifics with danger, and subsequently, on seeing a frightened conspecific with a snake, associate snakes with danger. This successive learning process is analogous to second-order conditioning; a two-stage associative learning process first described by Pavlov (1927), which has since been demonstrated in a wide range of animal taxa, including humans (Jara et al., 2006), rats (Holland and Rescorla, 1975), sea slugs

(Hawkins et al., 1998), bees (Hussaini et al., 2007) and flies (Tabone and de Belle, 2011).

Bumblebees are known to ‘copy’ flower choices by observing foraging conspecifics from behind a clear screen (Worden and Papaj, 2005; Avarguès-Weber and Chittka, 2014). Second-order conditioning might explain this finding if bees first learn to associate conspecifics with food, then associate conspecifics with the flower species in question, leading to a secondary association between food and the flower type (figure 2.1). We tested this hypothesis by exposing bees to alternative first-order associations, whereby conspecifics were either associated with sucrose or bitter quinine, or, were excluded from forming associations with conspecifics altogether. We predicted that bees would only copy flower colour choices if previously trained to associate conspecifics with rewarding sucrose, while those without such experience would not. In contrast, bees that associated conspecifics with punishing quinine should avoid flower colours on which demonstrators were previously seen (figure 2.1).

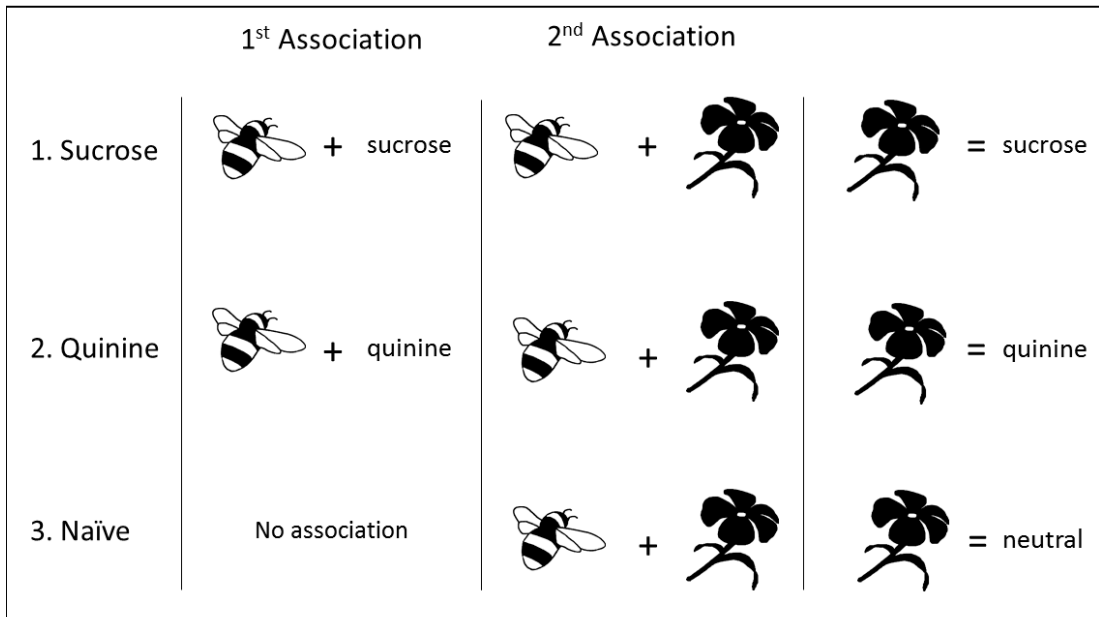


Figure 2.1 How flower colour copying in bumblebees might emerge from a two-step associative process. (1) In the sucrose group, bees first associate conspecifics with rewarding sucrose solution. Conspecifics are then seen on a particular flower colour. Subsequently, the flower colour and sucrose become associated which might lead to ‘copying’ behaviour. (2) The reverse should be true if conspecifics are associated with aversive quinine, resulting in bees avoiding the flower type. (3) If no association occurs with conspecifics, the flower should be neither positively or negatively valued and bees should therefore neither copy nor avoid demonstrator flower colour preferences.

2.3 Methods

(a) Test subjects & arena

Eleven bumblebee (*Bombus terrestris*) colonies, obtained from Syngenta Bioline Bees (Weert, the Netherlands) were used throughout the experiment. Colonies were housed in wooden nest boxes (28 X 16 X 11cm) that were connected to a flight arena (117cm X 72cm X 30cm) by a Plexiglas tube. Prior to experiments, bees fed from gravity feeders placed within the nestbox. Since nestboxes are dark, bees had no prior opportunity to form associations between food and conspecifics.

(b) Phase one: Training

Within the arena, individual motivated foragers were trained to feed from six transparent platform feeders (1.5cm X 1cm X 1.5cm; two vertical rows of three platforms attached to a brown cardboard background; figure 2.2(a)). Three of these six platforms were occupied by nine conspecific ‘demonstrators’; three demonstrators per platform. Two demonstrators were pinned to each side of the platform and one dangling by a short piece of thread from a pin to allow movement when a fan (‘The Cooler’ by ‘Design-Go’ 8.5cm X 4.5cm X 4cm) was turned on (figure 2.2(a)). The remaining three platforms were unoccupied. We used both model and unrelated dead conspecifics as the demonstrators in our experiment. Bees were killed by freezing one day prior to experiments and defrosted at room temperature just before experiments began. Models were made from oven-baked clay (Fimo soft, Staedtler) painted to match the reflectance of natural *Bombus terrestris* models, according to the bee’s visual spectrum (Chittka, 1992). Models were used to avoid

killing excessive numbers of bees, and previous social learning studies have demonstrated that bees and models elicit equivalent responses (Worden and Papaj, 2005; Leadbeater and Chittka, 2007a).

In the sucrose treatment group, demonstrator occupied platforms contained 20 μ l of 2M sucrose solution and unoccupied flowers contained 20 μ l of saturated quinine hemisulphate solution. In the quinine treatment group, occupied flowers contained quinine and unoccupied flowers contained sucrose. Subjects in the naive group were only presented with unoccupied platforms, half of which were rewarded with sucrose, while the other half contained quinine. The test bee was allowed eight foraging bouts from the feeding array; each time the position of the occupied and unoccupied platforms was changed to avoid subjects solely learning the position of rewarding flowers. Platforms were replenished every time they were depleted and the number of lands to occupied and unoccupied flowers was recorded.

(b) Phase two: Observation

The observation phase was designed to replicate the set-up used by Worden & Papaj (Worden and Papaj, 2005). After the test subject returned from offloading its sucrose load from the last foraging bout of the training phase, it was confined to an observation box attached to the side of the arena (30cm X 21cm X 22cm). In this observation box, test subjects could view the feeding array at a distance of 11cm away through a UV-transparent Perspex screen (21 X 22cm). The training feeding board was replaced with a similar array, where each feeding platform was now placed against a coloured “flower”. These six flowers consisted of three green and

three orange or three blue and three yellow circles (57mm diameter) against a brown background. The flower colour combinations were positioned randomly, again in two vertical rows; three flowers in each row. The contrast between each colour and the background, calculated in a colour space for bees (Chittka, 1992), was slightly higher for blue (0.21) than for yellow (0.18), and moderately higher for orange (0.2) than for green (0.14), where the maximum theoretical contrast between any colour and its background is 1. Each feeding platform was filled with 20 μ l of water.

Three demonstrators were attached to one of the two colours in the same positions as described in the training phase setup. Once again, a fan was used to move the hanging demonstrators. Test subjects were allowed to view the floral array, with demonstrators, for a period of 15 minutes. Halfway through this observation period, the position of the orange and green, or blue and yellow flowers was reversed, to ensure test subjects were associating demonstrators with flower colour and not flower location.

(c) Phase three: Testing

The final stage of the experiment involved testing for a subject's flower colour preferences. Immediately after the observation phase, the observed floral array was replaced with a new floral array, containing no conspecific demonstrators. Once again, the spatial position of the flower colours was changed and all feeding platforms were filled with 20 μ l of water. The test subject was released into the arena and the landing choices of the subject were recorded for a five minute period

following (and including) the first landing on a flower. If no landings were made within ten minutes of the subject being released, the test was stopped.

In total we trained over 250 bees, with 158 completing the entire experiment (n=54, 50, 54 in Sucrose, Naïve and Quinine groups respectively).

(d) Colour preference test

In the experiment, two different flower colour combination pairs were used: orange/green, and blue/yellow. To establish innate preferences we tested 30 naïve bees that had never previously encountered these colours before. We found that bees had a slight preference for orange over green and blue over yellow (means \pm standard errors: 0.64 ± 0.04 and 0.60 ± 0.05 respectively), most likely in response to the contrasts with the background. Since these preferences for orange and blue did not differ significantly from one another ($F < 0.01$, d.f. = 1, $p = 0.95$), we pooled data from the two choice tests and included ‘choice test’ as a predictor in each model (see below).

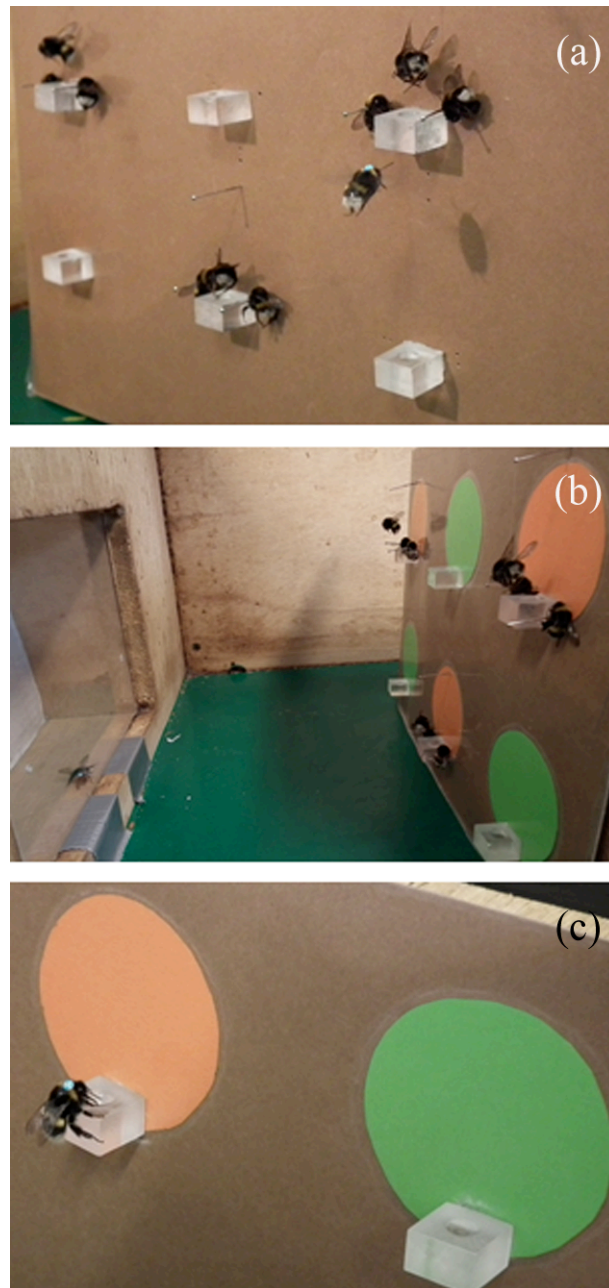


Figure 2.2 Photographs of experimental stages.

(a) Phase one shows the training phase where the test subject is required to associate conspecific occupied flowers with either sucrose or quinine. (b) During the observation phase, which occurred immediately after training, test subjects then observed demonstrators on one of the two flower colours. (c) The final phase involved testing the bee for its flower colour preferences in the absence of demonstrators.

(e) Analyses

To assess whether bees had learnt to associate conspecifics with sucrose or with quinine in the training phase, we compared the proportion of visits to the conspecific occupied flowers, in the last training bout, with chance expectations (0.5) using a one-sampled t-test.

For each treatment group we then modelled the proportion of landings to colour A in the test phase using a Generalised Linear Model with a quasibinomial error distribution to correct for overdispersion of residuals. We assigned orange/blue as ‘colour A’ since we found no significant difference in innate preferences for these colours (see section ‘Colour preference test’). We fit the position of demonstrators (Colour A or Colour B), choice test colour combinations (orange/green or blue/yellow), and proportion of correct choices in the final training bout as predictors in our model. Non-significant terms were dropped sequentially until further simplification significantly decreased the explanatory power of the model. P-values represent the effect of removing significant terms from the minimal model, evaluated using F-tests. All statistical analyses were carried out using R statistical software (v.2.12.0)

2.4 Results

Bees in both the Quinine and Sucrose groups successfully learnt the first-order conditioning task. On the final foraging bout of the training phase, bees in the Sucrose group visited conspecific occupied flowers significantly more frequently than chance expectation ($89 \pm 13\%$; one-sample t test: $t = 4.01$, d.f. = 49, $p < 0.001$),

while subjects in the Quinine group avoided conspecific occupied flowers and preferentially landed on unoccupied flowers ($93 \pm 10\%$; $t = 3.57$, d.f. = 52, $p < 0.001$).

We found that this first-order association was critical to whether bees copied demonstrator's flower colour preferences (figure 2.3). Subjects that had previously associated conspecifics with sucrose were significantly more likely to visit the flower colour they had previously seen demonstrators on than if demonstrators were seen on an alternative colour ($F = 5.27$, d.f. = 1, $p = 0.02$). Conversely, bees trained to associate conspecifics with quinine were more likely to choose a flower colour when demonstrators were seen on the alternative colour ($F = 4.23$, d.f. = 1, $p = 0.04$). Bees in the Naïve group, who did not undergo the first-order conditioning phase, were not influenced by the position of demonstrators and showed no significant preference for either occupied or unoccupied flower colours ($F = 1.21$, d.f. = 1, $p = 0.28$). Flower colour combinations (blue/yellow or orange/green) ($F < 1.0$, d.f. = 1, $p > 0.3$ for all treatment groups) and training performance ($F < 1.6$, df = 1, $p > 0.2$ for Sucrose and Quinine groups) had no effect on test choices.

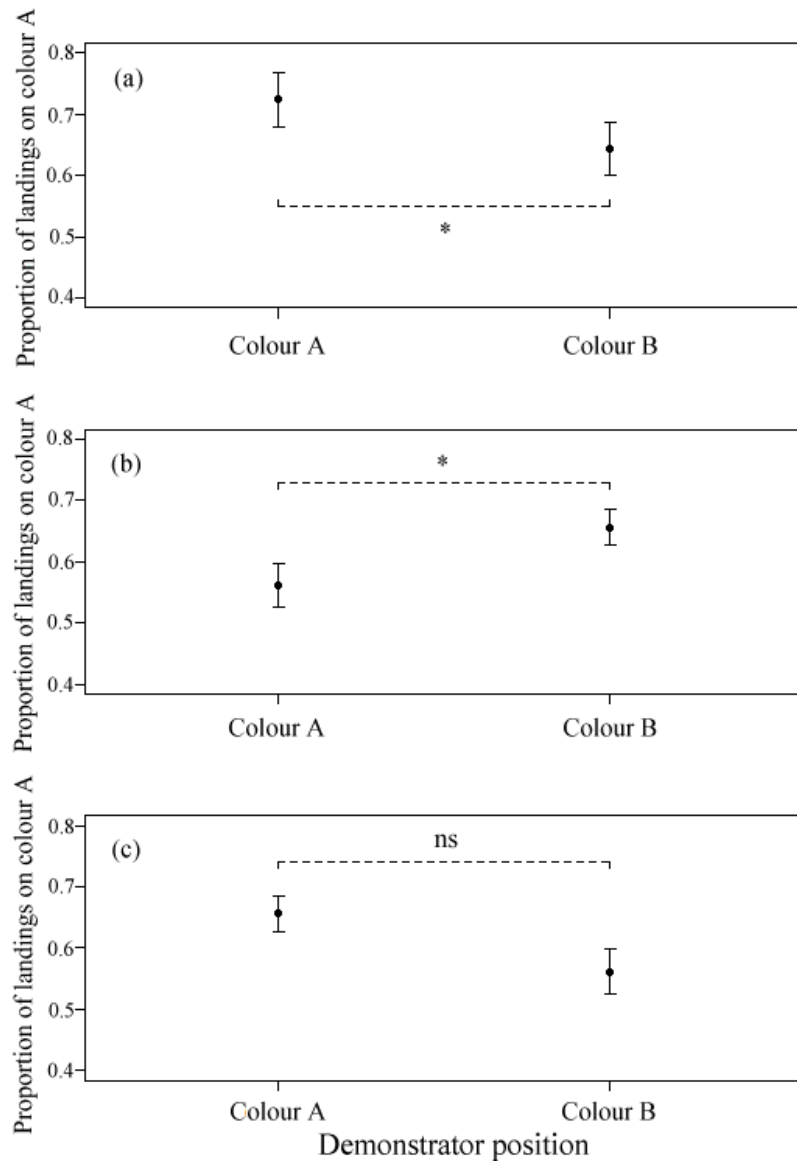


Figure 2.3 Graph showing the proportion of landings on Colour A (either orange or blue), when bees could view demonstrators on Colour A or Colour B, made by bees trained to associate conspecifics with (a) sucrose or (b) quinine, or (c) naïve bees that underwent no first-order association. * signifies $p < 0.5$, while ns indicates not statistically significant.

2.5 Discussion

As predicted by our hypothesis, the first-order association with conspecifics was integral in determining copying behaviour in bees. Bees that had previously learnt to use conspecifics as a predictor of food, copied demonstrator flower preferences, but bees without such associative experience did not, and those that had previously associated conspecifics with an aversive stimulus actively avoided demonstrator choices. Our findings demonstrate that learning by observing others does not necessarily demand specialised cognitive adaptations, but instead requires only the facility to integrate two associations, a feature common to both social and asocial animals (Holland and Rescorla, 1975; Jara et al., 2006; Hussaini et al., 2007; Tabone and de Belle, 2011).

Flower colour copying in bumblebees can be viewed as ‘observational conditioning’, where the presence of conspecifics feeding on a particular flower colour exposes the observer to an association between rewards and that colour. Alternatively this behaviour could also fall under the category of ‘stimulus enhancement’, in which attraction towards conspecifics exposes bees to a particular flower colour resulting in an increased interaction with that colour (Hoppitt and Laland, 2008). Both processes can be viewed in an individual learning framework, whereby an association is made between social cues and flower colour, yet there is a widespread assumption that animals have evolved to treat conspecific behaviour as a particularly relevant stimulus. We demonstrate that second-order conditioning requires no such adaptations and responses to conspecifics arise simply through individual learning mechanisms.

Typically animals are attracted to the presence of conspecifics in order to locate and identify foraging patches. Yet, if associative learning underlies the use of social information, then animals should also be capable of forming negative, as well as positive, associations with social cues (Heyes, 1994; Hoppitt and Laland, 2008). In other words, if the presence of conspecifics predicts the absence of food (e.g. through competition), animals should show an avoidance, rather than attraction, response. Our findings corroborate this by demonstrating that prior negative associations with conspecifics leads to avoidance behaviour in bees. In the wild, bees may frequently form negative associations with social cues since many flowers are often depleted by a single pollinating visit (Goulson et al., 1998; Leadbeater and Chittka, 2011). However, an aversive stimulus, such as quinine, may be stronger in eliciting an avoidance response in bees than simply the absence of food, and therefore, we should be cautious extrapolating our findings to an ecological context.

While our data demonstrate that social and asocial processes can be mediated by the same learning mechanisms, we do not presuppose that learning by observation involves no specialized adaptations. An animal may be more motivated to be in closer proximity to conspecifics, or may perceive or pay particular attention to social behaviour, leading to a higher probability of first order associations occurring with social sources (Heyes, 2012). For example, some species of birds learn to sing by listening to the songs of other birds (Catchpole and Slater, 1995). However, this process is only successful if conspecific songs are heard; if heterospecific songs are used, a highly erroneous copy is produced (Konishi, 1985), demonstrating that these birds have an auditory template specially adapted for receiving information from their own species. Bumblebees are capable of forming associations with a wide array

of stimuli, yet do they possess specialised ‘input mechanisms’ which prioritise learning information sourced from conspecific individuals? In the next chapter, I will investigate this question by testing the strength of first-order associations made with various social and non-social cues.

Chapter 3: Conspecific and heterospecific information use in bumblebees

Data from this chapter are published, along with data from my MSc thesis, in the following publication. I emphasise that none of the data from my MSc dissertation are included in this thesis.

Dawson, E.H. & Chittka, L. 2012. Conspecific and heterospecific information use in bumblebees. *PLoS ONE* 7, e31444.

3.1 Abstract

The associative mechanisms that enable social learning are widespread in both social and asocial species. This raises the question of whether animals possess any specialised ‘input mechanisms’ that render conspecifically sourced information as more influential, or whether animals can simply use any cue that predicts fitness enhancing conditions, including those provided by heterospecific species. To determine how freely social information travels across species boundaries, we trained entirely naïve bumblebees (*Bombus terrestris*), that had never foraged alongside conspecifics before, to learn to use cues provided by conspecifics and heterospecific honey bees (*Apis mellifera*) to locate valuable floral resources. We found that heterospecific demonstrators did not differ from conspecifics in the extent to which they guided observers' choices, whereas a non-social cue, consisting of a black wooden block, was consistently less efficient than conspecific cues. This was also true in a transfer test where bees were confronted with a novel flower type. Our

findings demonstrate that while bees learn social and non-social cues to differing degrees, bees are undiscerning when it comes to learning conspecific and heterospecific information sources, highlighting that social learning is not a unique process limited to conspecific interactions.

3.2 Introduction

The use of socially acquired information allows animals the opportunity to bypass the costs associated with personal sampling of an environment. Yet, an inflexible use of socially sourced information does not intrinsically lead to the most optimal behaviour: if the number of social learners exceeds the number of asocial learners, the value of social information declines as up-to-date information about the environment is no longer sampled (Rogers, 1988; Giraldeau et al., 2002). Similarly, animals should also demonstrate selectivity when deciding *whom* to copy (Coussi-Korbel and Fragaszy, 1995; Laland, 2004; Seppänen et al., 2007). Indiscriminate copying may lead to over-exploitation of resources and severe competition, particularly among conspecifics whose niches wholly overlap (Seppänen et al., 2007). From this perspective, using information from heterospecific species with similar needs may offer a valuable alternative since there may be fewer competitive costs compared to those associated with conspecific species (Seppänen et al., 2007; Goodale et al., 2010). Furthermore, heterospecific individuals may differ in the way they acquire information, as well as their perception abilities. Therefore, information that is not readily attainable from personal sampling or conspecific sources could be obtained from heterospecific animals. Indeed numerous cases of learning across the

species boundary have now been documented. Many different animals, from a wide range of taxa, use information originating from heterospecific species to avoid predators (Brown and Laland, 2003; Rainey et al., 2004; Kitchen et al., 2010; Magrath and Bennett, 2012), locate food sources (Dolman et al., 1996; Whiting and Greeff, 1999; Coolen et al., 2003) and find habitats or nest sites (Seppänen and Forsman, 2007; Hromada et al., 2008; Forsman et al., 2012).

Since social learning largely relies on the same learning processes that underlie individual learning (Heyes, 1994, 2012), there should be no presupposition that learning from others is exclusively limited to intraspecifically sourced information. As long as the information reliably predicts rewarding or punishing outcomes, then the source of the information could just as equally originate from a different species. However, while social learning may not require any specialised learning mechanisms, selection may still have shaped an animal's ability to *receive* social information (Heyes, 2012). An animal may have a perceptual system more tuned to receiving conspecific information (Galef Jr et al., 1988; Marler and Slabbekoorn, 2004), as in some species of song birds who only have the capacity to learn songs from members of their own species (Marler and Peters, 1977), or who copy the songs of a heterospecific tutor to a worse degree than songs originating from conspecific individuals (Konishi, 1985; Clayton, 1989).

Bees often share their foraging environment with multiple species of pollinators (Waser, 1982; Waser et al., 1996) who, like conspecifics, could also inadvertently provide useful information regarding food resources. For example, a species of stingless bee, *Melipona rufiventris*, deposits odour marks to guide nestmates to profitable foraging sites. However, a competing species, *Trigona spinipes*, also

exploits this information and uses the heterospecific odour marks to locate and take over the food source (Nieh et al., 2004). Conversely, bumblebees and honeybees reject recently depleted flowers by detecting olfactory footprints left by both conspecific and heterospecific visitors (Stout and Goulson, 2001; Gawleta et al., 2005; Reader et al., 2005). The exploitation of these scent-marks arises through associative learning since naïve bees, with no previous foraging experience, do not display this avoidance behaviour (Leadbeater and Chittka, 2011), and if experienced in parallel with a reward, scent-marks, instead, act as an attractant on foraging bees (Saleh and Chittka, 2006). Yet, while bees are clearly able to process heterospecific social information, and use it in an adaptive manner, do bees still possess an input bias that renders conspecifically sourced information as more salient?

In this chapter, I address this question and explore whether bumblebees (*Bombus terrestris*) are specially adapted for learning conspecific information by assessing how subjects respond differentially to visual cues provided by conspecifics, heterospecific honeybees (*Apis mellifera*) and a non-social stimulus. By comparing learning performance, I illustrate that foragers learn conspecific and heterospecific cues to the same extent, but non-social cues are consistently learnt to a worse degree.

3.3 Methods

(a) Test subjects & arena

Seven bumblebee colonies were obtained from Syngenta Bioline Bees (Weert, the Netherlands) and housed in wooden nest boxes (28 x 16 x 11 cm) that were

connected to a flight arena (figure 3.1(a); 105 x 72 x 30 cm) by a Plexiglas tube. Only foragers newly emerged from the pupae were selected for experiments to control for any previous social foraging experience. Hives were fed by administering 50% (v/v) sucrose to honeypots and the colony was kept in complete darkness so as to avoid visual associations with rewarding sucrose and conspecifics. Once a motivated forager was identified, it was assigned to one of four treatment groups: Conspecific; Heterospecific; Non-social; or No Cue.

(b) Learning phase

Eight yellow artificial flowers (figure 3.1(a); 35mm diameter, craft foam circles, placed on top of glass vials, 50mm in height) were randomly placed around the flight arena. For bees in the Conspecific treatment group, a single dead (freshly freeze-killed), *B. terrestris* worker, taken from an unrelated colony, was placed in a foraging position on four of the eight flowers in the arena (figure 3.1(bi)). These cue occupied flowers were rewarded with 25 μ l of 50% (v/v) sucrose solution. The remaining four flowers were unoccupied and contained no reward. For the Heterospecific treatment, rewarding flowers were occupied by a single dead heterospecific species, a honeybee (*Apis mellifera*)(figure 3.1(bii)). Individuals used to provide social cues had been killed by placing them at -20°C a day before experimentation and defrosted at room temperature just before testing took place. Note that bees' visual spatial resolution is too poor to distinguish visually between a motionless worker sitting on a flower and a dead bee (Kapustjansky et al., 2010), and previous tests on within-species social learning have proven pinned, dead specimen

to be readily acceptable by bumblebee workers choosing flowers (Leadbeater and Chittka, 2009).

To explore whether any arbitrary cue associated with floral rewards might perform the same function as a social cue, we also used a non-social visual cue comparable in size to the social cues. For this non-social treatment, a group of bees were trained with a 3-dimensional wooden rectangular cuboid (14 X 6 X 6 mm) painted with a black paint that had the same low reflectance across the bee visual spectrum as the black body parts of a *B. terrestris* forager (figure 3.1(biii)) (Stelzer et al., 2010). In all trials with the No cue group, no cues were used and all eight flowers were rewarding. Bee subjects were allowed three foraging bouts during the learning phase, with the rewards in the cue associated flowers being replenished after each bout. The position of all eight flowers was changed after each bout to ensure that subjects did not simply learn the location of the rewarding flowers.

(c) Test 1: Yellow flowers with & without cues

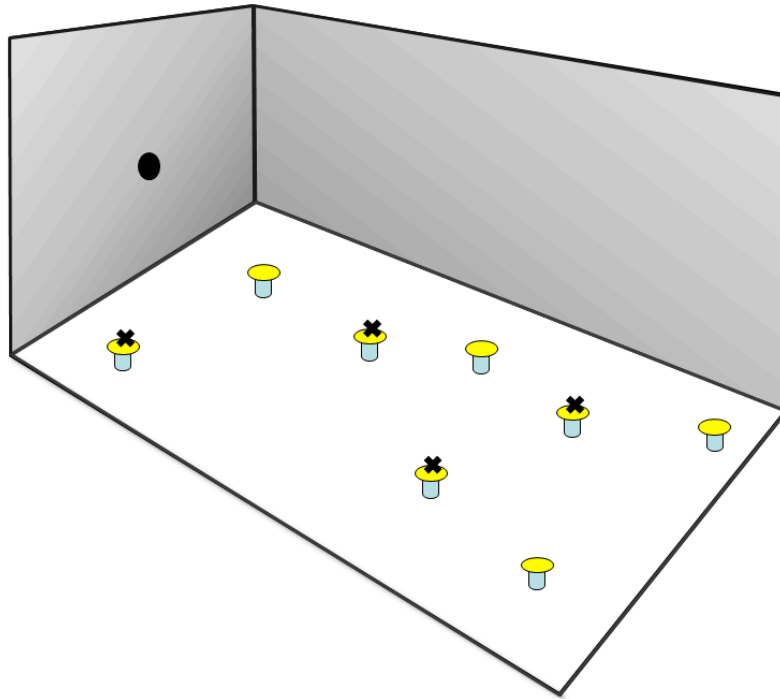
Testing took place straight after the third bout of the learning phase. All flowers were replaced with eight ethanol cleaned yellow flowers to eliminate any scent cues that may have remained from previous visits. Again, with exception of the No cue treatment, four of these flowers had a cue attached, while the remaining four had no attached cue. Demonstrators were also replaced with new dead specimens; non-social cues were cleaned with ethanol prior to tests. None of the flowers were rewarded to ensure that the number of visits reflected the subject's preference and was not just a result of revisiting rewarding flowers. To assess whether bee subjects

had learned to associate the specific cue with a reward, the number of visits to cue occupied and unoccupied flowers was recorded. A visit was defined as the subject landing on the flower. The test ended once the subject left the arena to return to the hive.

(d) Test 2: Transfer test with blue flowers

The second test ascertained whether bee subjects could then transfer the information that they had learnt in the learning phase to a new flower “species”. Immediately after test 1, cue occupied yellow flowers were rewarded again for a single foraging bout to reinforce the association that had occurred in the learning phase. Once the bee subjects returned to the hive to offload the sucrose solution, all yellow flowers were replaced with a new flower “species”; artificial blue flowers (35mm diameter, craft foam circles, placed on top of glass vials, 50mm in height). These new flowers were randomly distributed throughout the arena, with the appropriate cues attached. Again all the flowers were unrewarded. Since subjects only ever landed on cue occupied flowers, recording the proportion of landings on these cue occupied flowers did not give an informative indication of how well bees identified their respective cues on the new flower colour. For this reason, the time for each subject to land on the first blue cue occupied flower was recorded. The test finished when the subject left the arena.

(a)



(b)

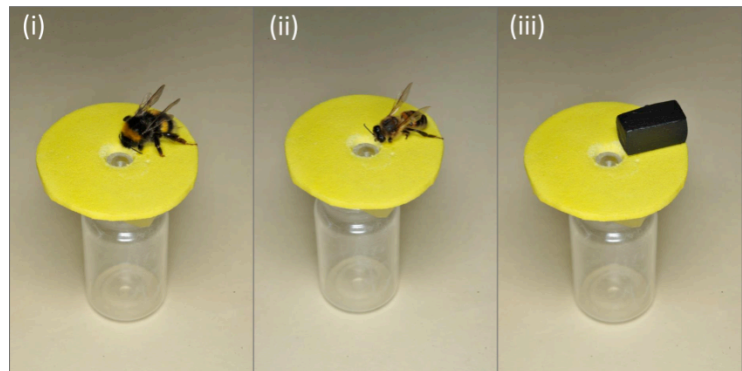


Figure 3.1 Experimental set-up. (a) A flight arena was set-up with eight yellow artificial flowers, (b) half of which were occupied by a dead (i) conspecific, (ii) heterospecific honeybee (*Apis mellifera*) or a (iii) non-social wooden cuboid.

(e) Analyses

To establish whether subjects in each treatment group learnt to associate their specific cue with a reward, the proportion of visits to occupied flowers in test 1 was compared against the chance expectation of visits to cue occupied flowers (0.5) using a two-tailed binomial test. To assess learning performance between the different treatment groups in test 1, the proportion of visits to cue occupied flowers was compared between treatments using a Generalised Linear Model with a quasi-binomial error distribution to correct for overdispersion. Only the first eight landings made by subjects were analysed. The No Cue treatment was excluded from this analysis as no cues were used and therefore proportion of landings to cue-occupied flowers could not be calculated.

A survival analysis using non-parametric Cox proportional hazard models was used to analyse latency times between treatment groups in test 2. Fifteen bees were tested within each treatment group, however subjects that made fewer than eight landings in test 1 were excluded from both analyses (Conspecific n=13; Heterospecific n=13; Non-social n=12; No cue n=15). All statistical analyses were carried out using the R statistical software (v.2.12.0).

3.4 Results

(a) Test 1: Yellow flowers with and without cues

Subjects in the social Conspecific, Heterospecific and Non-social treatment groups all learnt to associate a reward with their respective cues (figure 3.2); two-tailed

binomial test $p < 0.001$; $p < 0.001$; $p < 0.01$ for treatments Conspecific, Heterospecific and Non-social respectively). There was no significant difference in learning performance between subjects trained with conspecific and heterospecific cues (figure 3.2; $E = -0.6522$, T-value = -1.789 , $p = 0.0823$), indicating that both conspecific and heterospecific cues were learnt equally well. Subjects within the Conspecific treatment made significantly more landings on cue occupied flowers than subjects within the Non-social treatment group (figure 3.2; $E = -0.7735$, T-value = -2.103 , $p < 0.05$).

(b) Test 2: Transfer test with blue flowers

When faced with a novel blue flower type, subjects in the Conspecific treatment group had very similar latency times to subjects in the Heterospecific treatment group (figure 3.3; Z-value = -1.023 , $p = 0.307$), but significantly shorter latency times than subjects in the Non-social and No cue treatment groups (figure 3.3; Z-value = -2.685 , $p < 0.01$; Z-value = -3.923 , $p < 0.001$ for treatments Non-social and No cue respectively). The Non-social group had similar latency times to the No cue group (Z-value = -1.568 , $p = 0.12$), and thus was clearly a less efficient cue despite it having signalled reward with the same reliability as the social cues during the previous training on yellow flowers.

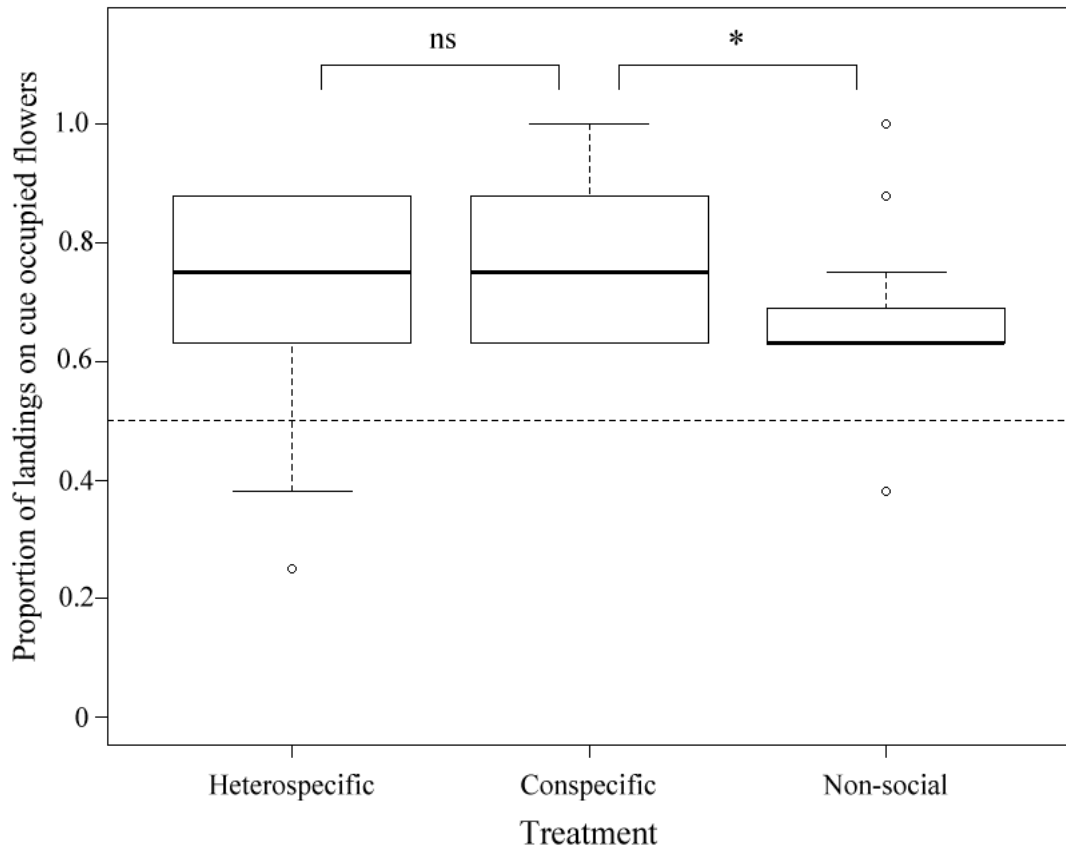


Figure 3.2 Proportion of visits to cue occupied yellow flowers. Medians, interquartile range and maximum/minimum values are indicated. * indicates between-treatment differences of $p < 0.05$, ns denotes no significant difference between treatment groups. Dashed line (0.5) signifies chance expectation of landing on cue occupied flowers (i.e. no learning has occurred).

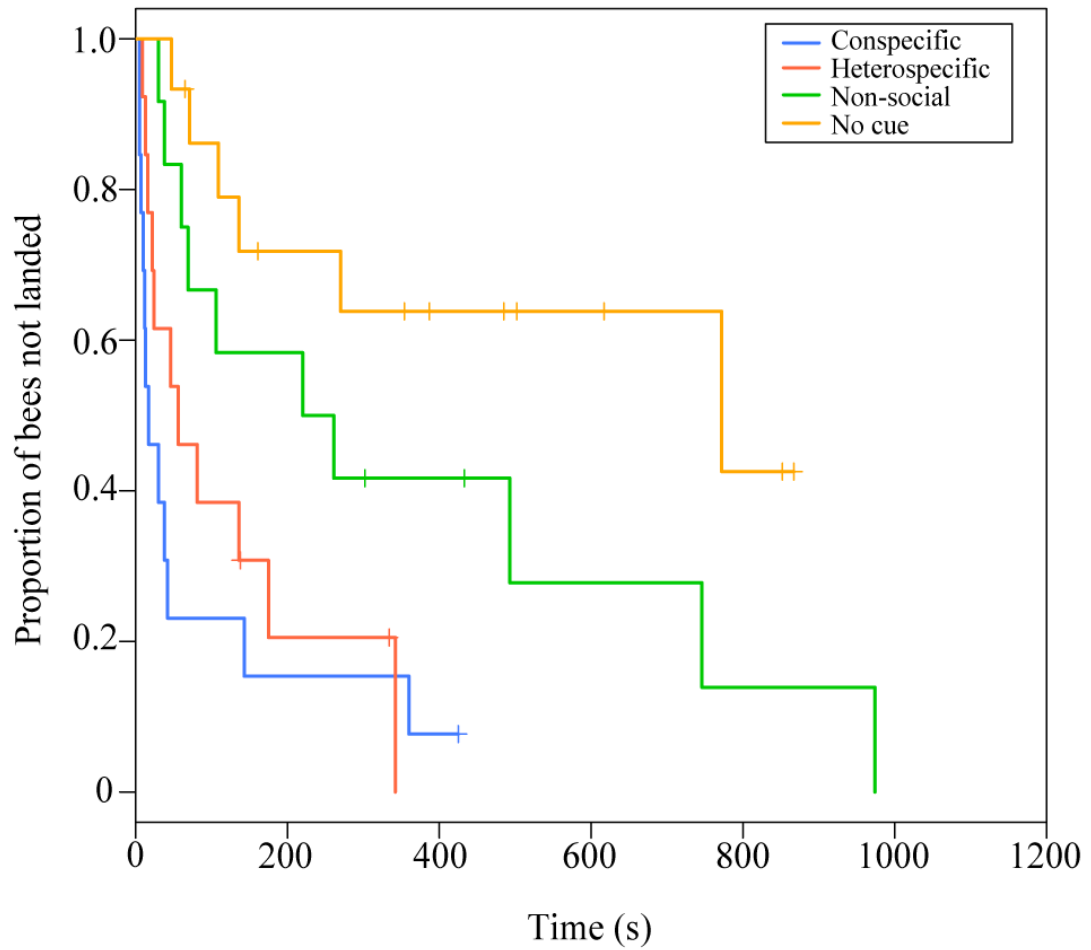


Figure 3.3 Transfer Test: Kaplan-Meier curves of latency times to land on blue flowers. Each step represents the time at which a bee landed and crosses throughout curves indicate where censoring occurred i.e. where a test subject left the arena without making a flower landing.

3.5 Discussion

We assessed whether bumblebees learn the heterospecific appearance on flowers as predictors of reward to the same degree as information provided by members of their own species, and found that this was indeed the case. This raises the question of whether any arbitrary cue, that is reliably associated with the same outcome, might be used with equal probability. However, we found that, as opposed to cues provided by heterospecific demonstrators, non-social cues bearing the same information were consistently less efficient than conspecifics as pointers to rewarding flowers, suggesting bumblebee workers appear to have a preparedness for accepting cues with a pollinator-like appearance over other cues that might, in nature, simply be part of the flower display.

The same overall picture holds in a transfer test, where subjects were faced with a novel target flower colour that they had never seen before. The only familiar cues on these new flowers were those that subjects had previously been exposed to in association with rewarding yellow flowers. In the transfer test, subjects most swiftly accepted flowers occupied with conspecific and heterospecific demonstrators, followed by flowers with non-social cues. When the novel flowers bore no familiar cue, subjects barely visited them at all over the testing period.

Our findings indicate that bees do not differ in their abilities to form associations with conspecific and heterospecific information sources. Yet, across the pollinator spectrum, bumblebee and honeybee foragers are relatively similar in appearance. It would therefore be interesting to investigate how bumblebees handle information sourced from a pollinator that significantly differs in taxonomy or morphology, such

as a butterfly. Furthermore, natural selection may have influenced other mechanistic input biases, not investigated here, which promote conspecific social learning. For example, bumblebees may have specially adapted motivational systems that predispose them to be in closer proximity with conspecifics, increasing the opportunity for social learning to occur between members of the same species (Heyes, 2012; Lotem and Halpern, 2012).

Previous research indicates that the saliency of conspecific information in bumblebees is influenced by past social foraging experience (Dawson, 2010; Dawson and Chittka, 2012). In an identical experimental set-up, it was found that bees, that had the opportunity to forage with nestmates prior to experiments, learnt conspecific visual cues more efficiently than heterospecific honeybee cues (Dawson, 2010; Dawson and Chittka, 2012). This difference in learning abilities highlights that specialised adaptations for receiving conspecific information need not necessarily arise through genetic adaptations (Heyes, 2012), since bees only prioritised information from their own species *after* past foraging associations with nestmates. A similar finding was demonstrated in two populations of Zenaida doves (*Zenaida aurita*). The population that foraged alongside conspecifics were more likely to learn from members of the same species, whereas the population that foraged antagonistically with conspecifics were more likely to learn from a sympatric heterospecific species, the Carib grackle (*Quiscalus lugubris*)(Dolman et al., 1996). Importantly, these two populations were not genetically different suggesting that the propensity to learn preferentially from conspecifics arises through ontogenetic, rather than genetic, processes (Heyes, 2012).

Whether bumblebees use and learn heterospecific sourced information to the same degree as conspecific information in the wild requires further investigation. However, the conditions in this experiment most likely represent those of a wild colony, where foragers emerge singly from the colony and fly long distances to flowers (Goulson, 2003). In such conditions, foragers are unlikely to encounter conspecifics on flower patches exclusively. Therefore it seems likely that wild bees would have opportunities to learn heterospecific and conspecific information to an equal degree. Since generalist pollinators, such as those under investigation here, typically share many flower species (Waser, 1982; Waser et al., 1996), using information provided by heterospecific species could often help bees identify rewarding flowers. This is especially the case for inflorescences that contain many nectaries in a single display, such as sunflowers (*Helianthus annuus*), that will often be fed from by multiple pollinators simultaneously (Leadbeater and Chittka, 2009) (figure 3.4). Furthermore, our findings also suggest that heterospecific cues, once they have been learnt as predictors of reward on one flower species, can facilitate the sampling of new flower species. As opposed to some stingless bees (Lichtenberg et al., 2011), bumblebees are not known to engage in active interference competition; they do not displace each other from flowers by overt aggression.

My findings demonstrate that under similar learning conditions, heterospecific social learning is not only possible, but also as efficient as that of conspecific social learning, suggesting that bumblebees possess no specialised adaptations for processing information pertaining to members of their own species.



Figure 3.4 A bumblebee (*Bombus terrestris*) and honeybee (*Apis mellifera*) foraging from the same sunflower inflorescence (*Helianthus annuus*). Photograph by Annurudha Jaithirtha.

Chapter 4: A field exploration of social information use in bumblebees

4.1. Abstract

Bees have been shown to exploit social cues in a wide array of situations: from locating food to avoiding predators. Yet, these experiments are often performed under laboratory conditions, which are not always fully representative of a bee's natural foraging environment. Here we investigate how free-flying bumblebees (*Bombus soroeensis*), in the Italian Alps, use social cues in order to make foraging decisions. We presented bees foraging on brown knapweed (*Centaurea jacea*) inflorescences with the choice of landing on one of two flower heads of the same species, one of which was occupied by a model conspecific, and found an overwhelming avoidance response towards occupied inflorescences. However, when bees, foraging on a different flower species, (creeping thistle [*Cirsium arvense*]), were offered occupied or unoccupied brown knapweed flower heads, conspecifics were no longer avoided, and bees chose between occupied and unoccupied flowers at random. I discuss these findings in light of the costs and benefits which social information use elicits.

4.2 Introduction

The use of social information by bumblebees has been extensively explored in laboratory settings and through these efforts we have learnt much about the circumstances under which bees employ personal and social information (Leadbeater and Chittka, 2005, 2009; Baude et al., 2011; Dawson and Chittka, 2014; Leadbeater and Florent, 2014). However, a bee's natural environment is multi-dimensional, where many different variables, such as predator risk, food availability and competitive costs are not always realistically represented in a lab setting, and therefore any observed behaviour may not necessarily be a direct reflection of behaviour in the wild (Kendal et al., 2010). In this chapter, we explore how free-foraging bumblebees use social information when choosing flowers in their natural environment.

Bumblebees often face an unpredictable floral market in their natural foraging environment, where different flower species become available at different times (Heinrich, 1979). In order to keep abreast of these changes, bees are required to continuously sample flowers within their habitat. Yet, this is not always the optimal strategy, since a trial-and-error approach often incurs weighty energy and predation costs (Laland, 2004). In this view, using social information could offer a more efficient strategy since individuals can substantially lower these costs by directly obtaining the relevant information through the behaviour of other individuals (Galef Jr and Giraldeau, 2001).

Bumblebees have been shown to exploit conspecific scent-marks (Goulson et al., 2000), alarm products (Goodale and Nieh, 2012; Llandres et al., 2013) or the

presence of other bees to locate food sources (Worden and Papaj, 2005), handle flowers (Leadbeater and Chittka, 2008) and avoid predators (Goodale and Nieh, 2012). While these inadvertent social cues can be either attractive, leading to joining behaviour with conspecifics (Leadbeater and Chittka, 2009), or repelling, causing avoidance behaviour (Goulson et al., 1998; Stout and Goulson, 2001), the presence of bees on flowers can also often elicit both responses, conditional upon the environmental contingency (Saleh and Chittka, 2006; Kawaguchi et al., 2007). For example, in the following chapter, I show that bumblebees join conspecifics in situations where they perceive a threat, but ignore these visual cues when danger is no longer detected (Dawson and Chittka, 2014). The response outcome is largely dependent on the trade-offs that each behaviour entails. Joining conspecifics may be more advantageous if there is a high pay-off, such as locating profitable resources more quickly (Kawaguchi et al., 2006; Dawson and Chittka, 2012), while there may be more benefit in avoiding social cues if there are associated costs with joining behaviour, such as increased competition or diminished resources (Inouye, 1978; Thomson et al., 1987; Makino and Sakai, 2005).

Here we investigate whether an alpine species of bumblebee, *Bombus soroensis*, uses the presence of conspecifics on flowers to make foraging decisions in their natural environment. The nectar content of many flowers is quickly depleted by a single pollinator visit (Comba et al., 1999), and in such a scenario, joining conspecifics on a flower may not result in optimal behaviour (Williams, 1998). Conversely, due to the unpredictable environment in which bees forage (Heinrich, 1979), with flower species changing in reward levels at different times, joining conspecifics could lead to the discovery of rewarding flower species (Leadbeater and

Chittka, 2005; Kawaguchi et al., 2007). Furthermore, many species of inflorescences contain many flowers in the same floral display, or in close proximity to one another, resulting in the availability of multiple nectaries which may not be immediately depleted by a single pollinator.

We offered foraging *B. soroeensis* individuals a dual choice between landing on either a conspecific occupied or unoccupied brown knapweed inflorescence (*Centaurea jacea*). We tested males and females already foraging on brown knapweed and bees foraging on a different species, creeping thistle (*Cirsium arvense*), to investigate whether joining behaviour was conditional upon situations where flower species were familiar and potentially unfamiliar. In line with previous findings, we expected occupied inflorescences would be avoided when bees were familiar with the presented inflorescence, while bees foraging on a different flower species, are expected to use social cues to identify novel resources and join conspecifics (Kawaguchi et al., 2007).

4.3 Methods

(a) Field sites

Data were collected from two separate sites located within the Parco dell'Adamello National Park, Val Camonica, Italy, throughout the first three weeks of August, 2012. Experiments were performed at two separate sites: 'River' located at an altitude of 1325m, and 'Tonale' (figure 4.1(c)), found 1.5km away at an altitude of 1685m.



Figure 4.1 (a) Test subjects were offered brown knapweed flower heads through the interview stick. A *B. sorooensis* model was pinned to one of the two flowers (right side flower in the picture). (b) The interview stick was presented to test subjects foraging on the same flower species as interview stick inflorescences (brown knapweed) or a different unfamiliar flower species, creeping thistle (as shown in picture). (c) The ‘Tonale’ field site.

(b) Experimental procedure

Bombus soroeensis was used as focal species since it was the most abundant bumblebee species at our field sites. We presented free-foraging bees with a choice of landing on two inflorescences, one of which was occupied by a conspecific bee. To do this we used an ‘interview stick’ (Thomson, 1981; Kawaguchi et al., 2007); a 1m wooden stick with a forked end where individual flower heads could be placed at a distance of 10cm apart from each other (figure 4.1(a)). We chose brown knapweed inflorescences (*Centaurea jacea*; figure 4.1(a)), a herbaceous perennial plant native to Europe, as our flower options and ensured that both flower heads were of a similar size. For our model, which was attached to one of the two flowers, we used dead *Bombus soroeensis* workers (figure 4.1) collected from Hohe Tauern National Park, Austria by Dr Johannes Spaethe the previous summer. In order for models to be used repeatedly, these bees had been immersed in hexane (100%) for a one-week period, before being left to air dry so as to eliminate all odours and pheromones (Svensson and Bergström, 1977; Svensson and Bergström, 1979).

We randomly selected bees with a colour pattern similar to *B. soroeensis*, foraging on flowers at our field sites and offered them the interview stick, holding it so that the occupied and unoccupied flower were at an equal distance from the test subject (approximately 6cm). We then recorded whether the bee landed on the occupied or unoccupied inflorescence and noted which species of flower test subjects were foraging on before being offered the interview stick. Many species of alpine bumblebees are only reliably identified through invasive methods (microscope, dissection, molecular methods). To minimise disruption to this wild population of bees we therefore classified test subjects according to their colour patterns. While *B.*

soroensis shares a similar morphology and colour pattern with several other species, including *B. lapidarius* and *B. ruderarius*, it is unlikely that a test subject could differentiate between these species due to poor visual resolution (Kapustjansky et al., 2010).

Since the density of flowers was limited at our field sites, the interview flowers were only replaced after every four tests. To limit the effect of scent-marks (cuticular hydrocarbon footprints) left by previous test subjects, we alternated which flower the model was pinned to after each choice and subsequently found no effect of replacing flowers after every four trials (binomial GLM $\chi^2 = 0.99$, d.f. = 1, $p = 0.32$). In order to avoid re-testing the same individuals, we marked each subject with a small dot of oil based paint on the thorax before releasing it.

(c) Statistical analyses

To determine whether bees avoided or preferred the model occupied flower, we compared the number of bees landing on the occupied flower against 50% chance using a two-tailed binomial test. This test was carried out for subjects that had previously been foraging on the same (hereafter referred to as ‘same species’) and different species (hereafter referred to as ‘different species’) to the ones offered by the interview stick. To ascertain whether the sex of the test bee, date, time of day, field site, flower age (the number of trials each test flower had undergone) and switching from one flower species to another influenced flower choice, we performed a Generalised Linear Model (GLM) using a binomial error distribution. We fitted all terms and their interactions as predictors and dropped each term

sequentially until further simplification led to a decrease in explanatory power of the model. In our final analyses, we included *B. soroensis* females (n=203) and males (n=81) as our test subjects that had previously foraged on the same (brown knapweed), or different species (creeping thistle) to our test inflorescence.

4.4 Results

Both male and female *B. soroensis*, presented with the same flower species to which they had previously been foraging on, significantly avoided the inflorescence occupied by the conspecific model (figure 4.2; mean preference for occupied flower, 0.36, binomial test $p < 0.001$ [female], 0.21, binomial test $p < 0.001$ [male]), preferring to land on the unoccupied flower. However, when both male and female *B. soroensis* encountered an inflorescence of a different species to which they had been foraging on, they no longer demonstrated an avoidance response towards occupied flowers but instead showed no preference for either flower (figure 4.2; mean preference for occupied flower, 0.62, binomial test $p = 0.256$ [female], 0.54, binomial test $p = 0.88$ [male]).

Accordingly, we found that flower species (same or different) had a significant effect on landing choices (binomial GLM $\chi^2 = 17.86$, d.f. = 1, $p < 0.001$). The sex of test subjects, date, time of day, site and age of test flowers had no influence on trial outcomes (sex: binomial GLM $\chi^2 = 3.37$, d.f. = 1, $P = 0.06$; time of day: $\chi^2 = 0.13$, d.f. = 1, $P = 0.72$; date: $\chi^2 = 1.07$, d.f. = 1, $P = 0.3$; Site: $\chi^2 = 2.37$, d.f. = 2, $P = 0.3$; flower age: $\chi^2 = 0.99$, d.f. = 1, $P = 0.32$).

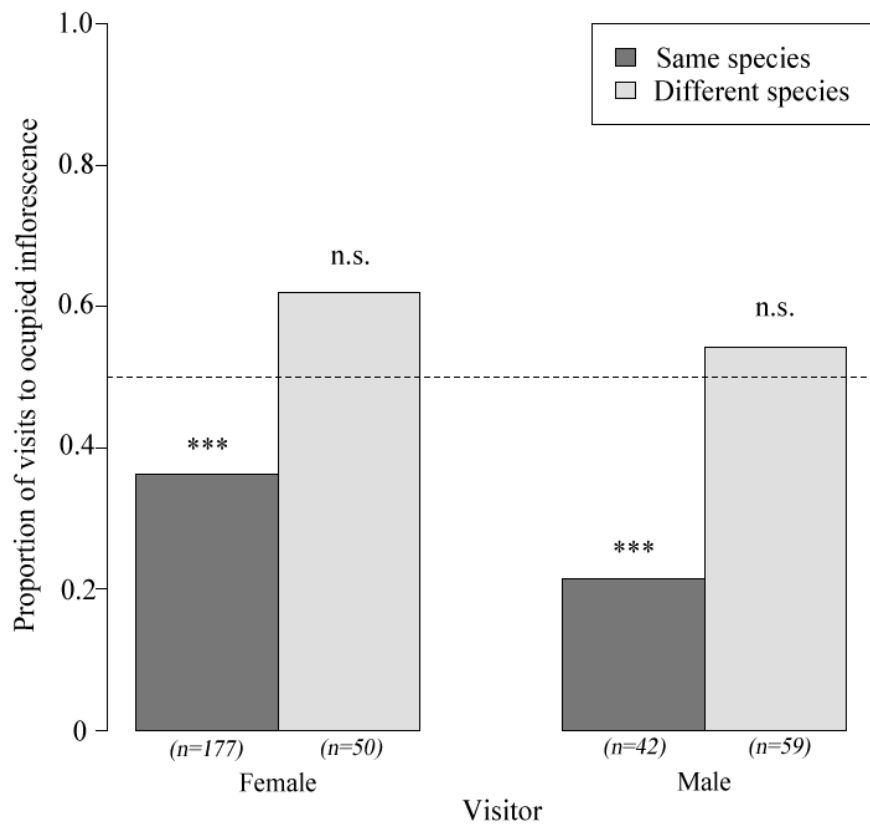


Figure 4.2 Proportion of landings male and female *B. soroeensis* subjects made on conspecific model occupied flowers which were either of the same (dark grey bars) or different (light grey bars) flower species to the one visitors were previously foraging on. Sample sizes are indicated in brackets. The dotted line shows the chance expectation of bees landing on the occupied flower. N.s. signifies landings on occupied flowers were not statistically different from chance, *** indicates $p < 0.001$.

4.5 Discussion

We found that in a natural environment, the use of social information by *B. soroensis* is context dependent: when bees approach the same flower species on which they were already feeding, they avoid visiting inflorescences occupied by other conspecifics; yet, when they encounter a different flower species, they choose their flowers at random, irrespective of whether the flower is occupied by another bee or not.

These findings are in accordance with previous field and lab studies which demonstrate that pollinators typically avoid joining conspecifics at familiar food sources (Slaa et al., 2003; Leadbeater and Chittka, 2005; Kawaguchi et al., 2007). Since flowers often provide only enough nectar for a single pollinator visit, conspecific presence at a food source may reliably indicate a flower depleted of nectar and allow bees a means of bypassing unprofitable flowers without expending energy on personal sampling (Baude et al., 2011).

However, what remains less clear is why bees ignored the presence of conspecifics when switching to a different species of inflorescence. Since our test subjects were free-foraging bees, we could not control for past foraging experience and therefore it was not possible to determine whether they had previously fed from our experimental flower species. As both flowers (creeping thistle and brown knapweed) were found concurrently at our field sites, and were visited by *B. soroensis*, we might conclude that our test subjects were familiar with both flower species and should therefore avoid the occupied inflorescence (Kawaguchi et al., 2007). Yet, the

response of test subjects does not reflect this scenario since bees were not deterred by the presence of conspecifics on the test inflorescences.

Alternatively, many bees display flower constancy, predominantly foraging from one flower species or type alone (Thomson, 1981; Chittka et al., 1999), which could result in the exclusion of other sympatric flower species. In this scenario, bees foraging on creeping thistles may have been unfamiliar with brown knapweed inflorescences, potentially explaining why an avoidance response was not found. Previous studies have shown that when food sources are new or unfamiliar, animals are more likely to join conspecifics (Slaa et al., 2003; Leadbeater and Chittka, 2005; Kawaguchi et al., 2006; Kawaguchi et al., 2007), potentially minimising the costs of individual exploration (Giraldeau and Beauchamp, 1999; Danchin et al., 2004). Yet, unlike these previous studies, we found that when bees switched flower species, there appeared to be neither an overriding avoidance *nor* attraction response towards the occupied inflorescence. This apparent lack of preference could simply reflect an amalgamation of bees with different foraging experiences: those familiar with brown knapweed, who should avoid the occupied inflorescence, and those with no previous experience of brown knapweed, who should be attracted towards conspecifics. Alternatively, instead of joining conspecifics directly, known as local enhancement, bees may have been employing a stimulus enhancement strategy (Heyes, 1994; Hoppitt and Laland, 2008), whereby the presence of conspecifics on the new flower species, brown knapweed, caused attraction to all inflorescences of that type, hence elucidating why both occupied and unoccupied flowers were chosen with equal probability.

While we found that all our visitors reacted in a similar manner towards occupied flowers, we should take caution when interpreting these results from a species perspective. Since we could only identify bees based on colour morphology, test subjects categorised as *B. soroeensis* may have been incorrectly grouped. *B. soroeensis* shares a very similar morphology and colour pattern with several other alpine *Bombus* species including *B. lapidarius* and *B. ruderarius* and can only be distinguished under a microscope. All volatile odours were removed from our demonstrator bees and their species membership should have only been identifiable through visual appearance alone, although colours may still have differed in spectral reflectance between the species.

Interestingly, we found that male bees used social information in a similar manner to female workers. Traditionally, research on male bumblebee behaviour has focussed on mating behaviour. From this perspective, it might be expected that males would either show a disproportionate attraction towards conspecifics (if they locate potential mates by visual cues, (Alcock, et al. (1978)) or ignore visual social cues altogether (if using alternative cues such as pheromones (Krieger et al., 2006)); however, we found that males were comparable to females in their approach to using social information. As bumblebee males rely on self-provisioning to fuel their mate search, requiring frequent recurring flower visits, optimising their exploitation of the floral market by using available social cues may be highly adaptive (Ostevik et al., 2010; Wolf and Moritz, 2014). Therefore, social information pertaining to floral rewards may be an important factor in the foraging decisions of both worker and male bumblebees.

To summarise, I have demonstrated that in addition to laboratory settings, bumblebees also use social information in their natural foraging environment. When male and female bees choose an inflorescence type with which they are already familiar, conspecific occupied flowers are avoided, potentially reducing competition costs. Conversely when bees switch to a different flower species, the presence of conspecifics no longer acts as a deterrent which may reflect different foraging experiences in free-foraging bees.

Chapter 5: Socially acquired predator recognition in honeybees

5.1 Abstract

Learning who is dangerous and who is not is a highly risky undertaking that may result in substantial fitness costs through injury or death. Yet many animals can bypass these potential costs by employing social information to indirectly learn about the identity of dangerous predators. In this chapter we explore the role associative learning plays in socially acquired predator recognition in honeybees (*Apis mellifera*). Individual honeybees were exposed to an unfamiliar coloured light together with volatile conspecific alarm volatiles. Subjects only acquired a fear response towards the coloured light if it had been associated with the alarm volatiles; previous experience with the light, in absence of alarm volatiles, did not evoke this response, nor did previous association of alarm volatiles with a different coloured light. Our results highlight that through a simple classical conditioning paradigm, honeybees have the potential to use conspecific alarm volatiles to learn about unfamiliar predators, or predator related cues.

5.2 Introduction

Avoiding predators is central to an animal's survival and fitness. While some species have an innate fear response to certain natural predators (Coss, 1978; Csányi, 1985; Barros et al., 2002; Schel and Zuberbühler, 2009), others are required to learn about what predators to avoid (Curio et al., 1978; Mineka and Cook, 1988; Chivers and Smith, 1994a). In other cases, there can be an interaction between the two, in that an innate avoidance is not necessarily apparent initially, but animals show preparedness to learn certain cues naturally associated with predators faster than others (Curio et al., 1978; Cook and Mineka, 1990; Chivers and Smith, 1994a). Yet, building a knowledge base about which animals are dangerous and which are not is a hazardous task which may potentially carry high fitness costs through death or injury. In these risky circumstances, acquiring information about predators from other individuals could offer a safe alternative to obtaining predator information through direct first-hand experience.

Many animals use information from other individuals to learn about impending danger such as when a known predator is present (Rainey et al., 2004; Fallow and Magrath, 2010; Nieh, 2010). However, in socially acquired predator recognition, animals learn the *source* of that danger by using social information to identify unfamiliar predators. Such socially guided predator avoidance is taxonomically widespread, with evidence found in primates (Mineka et al., 1984), birds (Curio et al., 1978), fish (Chivers and Smith, 1998), amphibians (Ferrari et al., 2007) and insects (Wisenden et al., 1997). In some cases, the underlying learning mechanism has been suggested to be a Pavlovian ability to associate two stimuli (Heyes, 1994; Hoppitt and Laland, 2008) so that predator cues (conditioned stimuli) are

experienced in contiguity with conspecific alarm cues (unconditioned stimuli) resulting in a subsequent avoidance of the predator cues (Mineka and Cook, 1993, Heyes, 1994, Shettleworth, 1998). Such conditioning is not restricted to visual cues (Hoppitt and Laland, 2008). For example, fathead minnows (*Pimephales promelas*) show no innate reaction towards predatory pike (*Esox indus*) chemical stimuli (Chivers and Smith, 1994b). However, when the minnows are exposed to the pike cues in parallel with conspecific alarm substances (unconditioned stimulus), they subsequently exhibit a fear response towards the pike cues alone (conditioned stimulus) (Chivers and Smith, 1994b). By using this simple associative framework, animals can potentially easily identify new predators without exposing themselves to the risks associated with individual learning.

Nests belonging to social insects offer an attractive food source for many predators due to the high abundance of immobile brood and other food reserves. To defend the colony from these potential predators, many social insect species, including ants (Parry and Morgan, 1979), wasps (Jeanne, 1981) and bees (Breed et al., 2004), have evolved a highly efficient chemical messaging system which facilitates a synchronised and coordinated attack on potential threats. For example, when honey bees (*Apis mellifera*) detect a colony threat, volatile alarm volatiles are released from the sting gland which recruits nearby nestmates to defend the nest (Boch et al., 1970; Blum et al., 1978). These new recruits then seek out and attack any moving objects perceived to be a threat (Wager and Breed, 2000; Breed et al., 2004). Conversely, outside the nest environment, chemosensory alarm information appears to have the reverse effect, eliciting an immediate avoidance response in conspecifics. Balderrama and colleagues (1996) demonstrated that honeybees trapped or lightly

squashed in a vial produce alarm chemicals that deter conspecifics from also entering the vial. Furthermore, both honeybees and bumblebees are known to be repelled by cues that are associated with injury to conspecifics, such as the smell of their haemolymph (Goodale and Nieh, 2012), and other volatile signals, including alarm pheromones (Llandres et al., 2013), which, in a foraging context, could result in the rejection of flowers concealing predators, enabling the discovery of safe foraging patches.

In this chapter, we explore whether honeybees, using chemosensory alarm volatiles, can socially learn the cues associated with predator threat through a simple associative learning paradigm. We first verify that honeybees do in fact produce an unconditioned fear response towards conspecific alarm volatiles and then assess whether these volatiles can be associated with a novel predator to elicit an avoidance response. To ensure bees were not influenced by any innate fear responses, we specifically chose a neutral stimulus, a coloured light, as our predation cue. Following this, we hypothesise that bees will be deterred by the conspecific alarm volatiles and will only avoid the coloured light after it has been experienced together with these volatiles.

5.3 Methods

The general task of our experiment followed that of Balderrama et al. (1996) where individual honeybees were timed moving from one vial to another through the process of phototaxis (the movement towards light). In the first phase of the experiment, bees had the opportunity to associate alarm volatiles with a coloured

light (table 5.1). In the second phase, bees experienced the light alone, with no volatiles present (table 5.1).

(a) Phase one: Conditioning

Honeybee foragers (*Apis mellifera*) were caught upon returning from a foraging bout to a hive located at Queen Mary University of London throughout the month of October, 2013. Once caught, subjects were brought to the lab for experiments and placed individually in glass vials ('vial A'; 5.5cm X 2.5cm X 2cm). In the first phase of the experiment, honeybees in groups E1 and E2 were presented with a replicate glass vial ('vial B'; 5.5cm X 2.5cm X 2cm) that contained conspecific alarm volatiles. Following Balderrama et al. (1996), to obtain these volatiles we gently squashed a conspecific (taken from the same colony) in the vial with a 1cm³ piece of sponge for one minute before removing both the sponge and the bee and immediately connecting the vial to the test subject vial, via a transparent plastic tube (15cm X 2.5cm). At the end of the second vial, the test bee could see a blue or green light ("Flexi Lite" LED light by True Utility covered with 3 layers of green or blue cellophane sheets by Bright Ideas Marketing Limited, cut to size), which shone through the base of the vial containing the alarm pheromone. Subjects in all control groups, C1 and C2 (table 5.1) were exposed to the light stimulus but in the absence of any alarm volatiles. Once both vials were connected, a light-restricting black sheet was placed over vial A to encourage the honeybee to move towards the experimental vial through a phototactic response. We measured how long it took test subjects to move into the opposing vial, with the timer initiated as soon as the honeybee had entered the connecting tube and stopped once it had entered vial B.

Table 5.1 Summary of experimental treatments and predictions. Table displays the sample size (N) and experimental conditions subjects experienced in each treatment group. Treatment groups consisted of Experimental (E1 & E2) and Control groups (C1 & C2). Following our hypothesis, predictions of bee responses are also included. Groups below the dotted line mirror the experimental conditions above the line, except with the reverse colour paradigm (i.e. green lights instead of blue).

Treatment	N	Phase 1 light	Phase 2 light	Volatiles in phase 1	Familiar light	Prediction: latency phase 1	Prediction: latency phase 2
E1	10	Blue	Blue	Yes	Yes	Increase	Increase
C1	10	Blue	Blue	No	Yes	No effect	No effect
E2	10	Blue	Green	Yes	No	Increase	No effect
C2	10	Blue	Green	No	No	No effect	No effect

E1	10	Green	Green	Yes	Yes	Increase	Increase
C2	10	Green	Green	No	Yes	No effect	No effect
E2	10	Green	Blue	Yes	No	Increase	No effect
C2	10	Green	Blue	No	No	No effect	No effect

(b) Phase two: Test

Immediately after phase one, the bee was briefly removed from the apparatus and all equipment, including the vials and the connecting tube, were swapped with clean replacements. To test whether bees in treatment group E1 were more reluctant to approach the coloured stimulus than bees that had not experienced the alarm volatiles (treatment group C1), subjects were again presented with a vial illuminated by the same colour they had experienced in phase one, but this time in absence of any alarm volatiles (table 5.1). To ensure any observed avoidance response was not simply a result of alarm volatiles rendering bees more sensitised to all stimuli in general, another group of subjects (treatment group E2) were presented with an alternative light colour (either green or blue) to the one they had experienced in phase one. Subjects in the control groups (C1 and C2) were also presented with empty vials, illuminated by the green or blue lights (table 5.1). Once again the time to enter vial B was recorded.

Ten bees were tested within each treatment group (table 5.1), with a total of 80 bees used in the experiment. Each bee was only tested once and released after experimenting. To avoid retesting, subjects were marked with a small dot of oil-based paint before being released. All vials and tunnels were washed in ethanol and dried after each use.

(c) Statistical analysis

For all analyses, we modelled the log-transformed time it took bees to move from vial A into vial B using General Linear Models. We selected models by comparing

Akaike's information criterion (AIC) values between different models. A model was considered to be a better fit if the AIC value was lower by more than two units (Johnson and Omland, 2004).

In the first stage of our analyses, we aimed to confirm that honeybees do in fact produce an avoidance response towards conspecific alarm volatiles. Our response variable was latency to enter vial B in phase one. We compared a basic model, which contained the intercept, with candidate models that included the presence of alarm volatiles and the colour of the light stimulus as predictors (Table 5.2a).

The same procedure was carried out for establishing whether bees would subsequently show a reluctance to approach the light that had been associated with alarm volatiles in the first phase of the experiment. Here, our response variable was latency to enter the vial in phase two. The basic model incorporated the colour of the light stimulus presented in phase two (since we found it had an influence on latency in phase one) and was compared to candidate models which included whether bees were exposed to alarm volatiles in phase one, whether the presented light colour was familiar (i.e. the same light bees experienced in phase one) and their interaction (table 5.2(b)). If bees did not learn to avoid the coloured light, the basic model would demonstrate the best fit. If test subjects learn to become fearful in general, but not towards a specific light colour, we would find that the most appropriate model would only include previous exposure to alarm volatiles as a predictor. If bees specifically learn to fear the colour of light experienced in phase 1, the fear response will be limited to only one light colour and therefore the best fitting model will include whether the light was familiar, past exposure to alarm volatiles and their interaction. All analyses were carried out in R v. 2.12.0.

5.4 Results

In phase one, the best model to predict latency to enter the vial included whether the vial contained alarm volatiles (estimate: 0.74 ± 0.15 [standard error, [SE]]) and the colour of the light stimulus (table 5.2(a); estimate: 0.31 ± 0.15 [SE]). Bees took longer to enter the vial when it contained alarm volatiles (figure 5.1(a); mean latency $19.05s \pm 2.16$ standard error of the mean [SEM]) than when no volatiles were present (figure 5.1(a); mean latency $9.15s \pm 0.69$ [SEM]) confirming that conspecific alarm volatiles trigger an unconditioned avoidance response in honeybees.

In phase two, bees that had experienced the alarm volatiles in phase one only showed an avoidance response when the light colour they were presented with was familiar (figure 5.1(b); mean latency $18s \pm 2.41$ [SEM]). When the light colour was novel, bees were no more reluctant to enter the vial than if they had never experienced the alarm volatiles (figure 5.1(b); mean latency $8s \pm 1.05$ [SEM]). In phase two, an avoidance response was best predicted by the model which incorporated whether bees had previous exposure to the alarm volatiles in phase one (estimate: -0.02 ± 0.17 [SE]), whether the colour of the light stimulus was familiar or new (estimate: -0.28 ± 0.17 [SE]) and the interaction between them (table 5.2(b); estimate: 0.95 ± 0.24 [SE]).

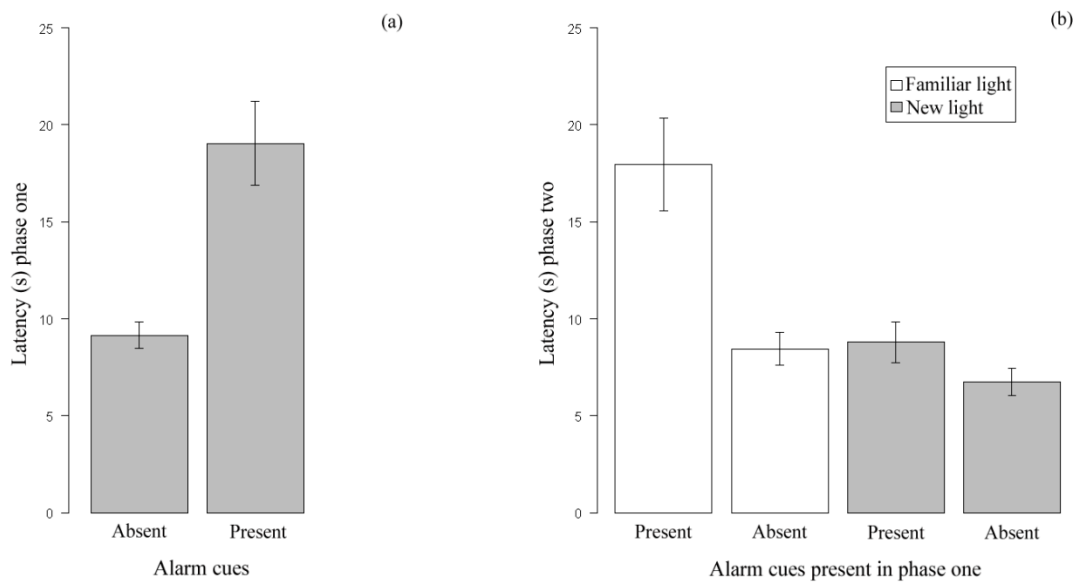


Figure 5.1 Mean (\pm SEM) latency times (s) for honeybees to enter vial B (a) in phase one, when alarm volatiles were either absent or present and (b) in phase two, when bees, that had or had not been previously exposed to alarm volatiles, were presented with a familiar (white bars) or novel (grey bars) light colour.

Table 5.2(a) Candidate models investigating the effect of various variables on the latency time to approach vial B for phase one. The best models (shown in bold) were selected based on the lowest AIC value. Δ AIC indicates the difference between that model and the best model.

model	AIC	Δ AIC
basic	192.2	20.4
pheromone	174.9	3.1
light colour	191	19.2
pheromone + light colour	171.8	0

Table 5.2(b) Candidate models investigating the effect of various variables on the latency time to approach vial B for phase two. The best models (shown in bold) were selected based on the lowest AIC value. Δ AIC indicates the difference between that model and the best model.

model	AIC	Δ AIC
basic	156.3	23.2
pheromone	146.6	13.5
familiar	156.3	23.2
pheromone + familiar	146.4	13.3
pheromone*familiar	133.1	0

5.5 Discussion

Our results support the hypothesis that alarm volatiles could facilitate the learning of new predators, or predator related cues, in honeybees. We found that bees acquired a fear response towards a novel light colour only after the light had been experienced in contiguity with conspecific alarm volatiles. Previous experience of the light alone did not evoke this response, nor did previous association of volatiles with a different light colour. This behaviour must occur through Pavlovian conditioning since the association between the coloured light and alarm volatiles was integral to honeybees displaying an avoidance response. Our findings provide further evidence that classical conditioning can be a simple and efficient process for predator avoidance learning in a wide array of different taxonomies (Mineka and Cook, 1993; Chivers and Smith, 1994a), including insects (Wisenden et al., 1997). In the social learning literature, such learning processes are sometimes referred to as ‘observational conditioning’ (Heyes, 1994; Hoppitt and Laland, 2008), though this term describes a wider range of learning processes, that can include simple associative learning as described here, but also second-order conditioning processes that do not require direct exposure to an unconditioned stimulus at the time of making some of the associations (Heyes, 1994; Leadbeater and Chittka, 2007b; Dawson et al., 2013).

We demonstrate that even cues not naturally pertaining to predators, such as a coloured light, can be conditioned to be feared, highlighting the flexibility of this learning process in honeybees. In a scenario where predators are cryptic or undetectable (such as crab spiders, sit-and wait ambush predators that lurk on flowers), this flexibility may be of benefit, allowing other features, such as flower location, to be learnt in order to avoid revisiting predator-infested foraging patches.

Conversely, an unselective approach to learning all predator associated cues could also result in maladaptive behaviour, with beneficial information potentially being misconstrued or used in the wrong context. However, many animals still demonstrate an inherent preparedness, or “filter”, for learning relevant predator cues more efficiently than arbitrary ones (Curio et al., 1978; Magurran, 1989; Cook and Mineka, 1990; Chivers and Smith, 1994a). So while we found that honeybees were capable of learning an arbitrary stimulus, a natural predator, such as a spider, may elicit a stronger or longer response.

Why do alarm volatiles elicit defensive behaviour at the nest, yet act as a repellent further afield? It has been postulated that two different pheromones may be responsible for the opposing behaviours, with defensive behaviours being triggered by an assortment of pheromones produced in the sting glands (Blum et al., 1978), and 2-heptanone, a mandibular gland pheromone, causing a deterrent effect (Simpson, 1966; Pickett et al., 1982; Vallet et al., 1991; Giurfa, 1993). However, in many cases of social insect pheromones, the response is dependent on context or past experience (Saleh and Chittka, 2006; Saleh et al., 2007) and therefore perhaps alarm pheromones only elicit an aggressive interaction under the right circumstances. For example, honeybees, on exposure to squashed venom sacs and sting apparatuses, produce a stereotypical increase in metabolic activity. Yet this response declines with decreasing group size (Southwick and Moritz, 1985; Moritz and Bürgin, 1987) suggesting reactions to alarm pheromones is contingent upon the environmental context.

An unconditioned response to conspecific alarm volatiles can be integral in triggering predator avoidance behaviour, yet this response need not necessarily arise

through specialised adaptations. Responses can be acquired through learning, where an individual directly experiences a predator in combination with conspecific anti-predator cues (Shriner, 1999). A secondary association can then occur between the alarm volatiles and a novel predator, through the process of second-order conditioning (Dawson et al., 2013), leading to the recognition of a new predator. In this learning framework, heterospecific anti-predator behaviours, which may not initially elicit an inherent response, can also be employed in learning to avoid unknown predators (Hauser, 1988; Rainey et al., 2004; Ferrari and Chivers, 2008). Bees exhibit a general avoidance response towards damaged heterospecifics (Goodale and Nieh, 2012) and we know that such associations can often be made freely across the species boundary (Dawson and Chittka, 2012), therefore there should be no reason why social learning of predators should occur between conspecifics exclusively.

To conclude, we highlight another context in which associations facilitate social learning. We demonstrate how honeybees can learn to recognise a novel predator through concurrent experience with conspecific alarm volatiles, thus allowing individuals to circumvent the costs of direct experience with potential danger.

Chapter 6: Using social information to locate safe foraging patches

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6.1 Abstract

Avoiding predation is one of the most important challenges that any animal faces. Several anti-predation behaviours can be employed, yet simply using the presence of conspecifics can be a good signal of safety in an environment with potential predation hazards. Here I show for the first time that past experience of predation causes bumblebees to aggregate with conspecifics, facilitating the identification of safe foraging patches. Bees were trained to differentiate between flowers that harboured predators and flowers that were predator free. When test subjects were subsequently presented solely with the previously predator-infested flower species, there was a significant preference to only land on flowers occupied by other feeding conspecifics. Yet, when safe flowers were made available to subjects previously entrained to discriminate safe from predator-occupied flowers, subjects ignored other bees and the social information potentially provided by them, demonstrating that attraction towards conspecifics is confined to dangerous situations. Our findings

demonstrate a previously unknown social interaction in pollinators which may have important implications for plant-pollinator interactions.

6.2 Introduction

Many animals have the capacity to glean information from other individuals in order to identify and locate potential predator threats. This could either be through direct communication about the threat (Zuberbühler et al., 1997; Zuberbühler, 2001; Leavesley and Magrath, 2005), detecting cues left by previous attacks (Dukas, 2001a; Abbott, 2006; Iglesias et al., 2012), or eavesdropping on anti-predator cues (Templeton and Greene, 2007; Schmidt et al., 2008). Yet, by using social information, animals can not only detect where danger lurks, they can also identify where danger is absent. While a dead or distressed conspecific might signify a potential threat, the presence of undisturbed conspecifics could just as importantly indicate an area free of predators, revealing a momentarily safe foraging opportunity. Indeed, many animal species aggregate with other individuals in response to predation pressures (Krause and Godin, 1994; Noë and Bshary, 1997; Côté and Jelnikar, 1999; Hoare et al., 2004), increasing the likelihood of spotting predators (Hamilton, 1971; Vine, 1971), as well as diluting the risks of being attacked (Kenward, 1978; Hoogland, 1981; Pays et al., 2013). Yet, despite the known advantages of group formation, it is still unclear what, if any, behavioural experience facilitates the attraction towards others in response to predation.

Recent research has highlighted the prevalence and importance of predation on pollinators and the consequences for pollination (Dukas, 2001a; Dukas and Morse,

2003; Suttle, 2003; Dukas, 2005; Reader et al., 2006; Gonçalves-Souza et al., 2008; Ings and Chittka, 2009; Jones and Dornhaus, 2011). Bees face significant predation threats from ambush predators that sit and wait for their prey, often on the flowers themselves. The best studied of these predators are crab spiders (Thomisidae), of which some species have the remarkable ability to change colour to camouflage themselves against the floral background (Chittka, 2001; Insausti and Casas, 2008). In order to evade these predators, bees can rely on personal information to avoid feeding on risky flowers. For example, since most crab spider predation attempts are unsuccessful (Morse, 1979, 1981, 1986), bees have the opportunity to learn and avoid the location of dangerous floral patches (Ings and Chittka, 2009). However personal sampling of an environment may impose severe fitness costs through predation risks, as well as significant reductions in foraging efficiency. Consequently there may be more benefit in using information from other individuals as a means to bypass these costs.

There is evidence that pollinating bees can indeed use social information to avoid predation either by identifying sites where other individuals have been attacked (Dukas, 2001a; Goodale and Nieh, 2012; Llandres et al., 2013) or by relaying the threat to nestmates (Nieh, 2010). Yet, these social strategies are not fail-safe since they will only account for instances where a predation attempt has just occurred, therefore leaving bees vulnerable to predators not recently engaged in a predator attack. Here I propose an alternative scenario, where bumblebees identify safe food sources by joining feeding conspecifics. Following this hypothesis, I predicted that through direct experience with a predator, joining behaviour in bees would vary with

subsequent predation threats: while in dangerous environments, joining would be more common than when foraging in safe environments.

6.3 Methods

(a) Set-up

Three bumblebee (*Bombus terrestris*) colonies (Syngenta, Weert, The Netherlands) were used over the course of the main experiment. Colonies were housed in nest boxes (29.5 X 40 X 11.5cm). Each test colony was sequentially attached to a wooden flight arena ($l= 100\text{cm}$, $w= 72\text{cm}$, $h= 73\text{cm}$) by a Perspex tunnel. Within the flight arena, bumblebees could forage from an artificial meadow which consisted of a 2 X 4 vertical array of eight flowers on a grey background (figure 5.1). Flowers had detachable colour signals which consisted of either yellow or white square plastic panels (7 X 7cm acrylic, 1mm thick, coloured white or yellow). Food (sucrose solution 50% w/w) could be accessed through a small circular hole 10mm above a landing platform (40 X 60mm). Landing platforms were flanked by two yellow foam-coated pincers (35 X 10 X 20mm white foam attached to the inside of grey wooden blocks 35 X 10 X 200mm) which could be rapidly closed to trap a bee briefly without the risk of injury to the bee (figure 5.1; (Ings and Chittka, 2008)).



Figure 6.1 Schematic diagram of the experimental artificial flowers. Sucrose could be obtained through the small hole. In this particular example, landing on white flowers results in the foam pincers closing (as indicated by black arrows) around the bee, while foam pincers remain open when a test subject lands on the alternative colour.

(b) Pre-training

Before training commenced, all bees from a colony were allowed to familiarise themselves with the floral array within the flight arena. To encourage bees to feed from the flowers, sucrose solution (1ml) was placed on the landing platforms, which was replenished frequently. In this phase, the detachable yellow and white colour panels were absent, so that flowers appeared the same colour as the grey background.

(c) Training to associate flower colours with reward or predation risk

During the training phase, all bees learned that they would receive a simulated predator attack on flowers of one colour while receiving no such attack on flowers of the alternative colour. Individual bees foraged in the meadow which now consisted of five 'safe' yellow flowers and three 'dangerous' white flowers. This colour paradigm was reversed for half the bees tested (i.e. white flowers were safe whereas visits to yellow flowers led to subjects being pinched). Every flower contained 5 μ l of sucrose solution, this time accessed via the feeding hole. To ensure subjects visited all available flowers, sucrose solution was only replenished after the subject had landed on all the safe flowers. When a test bee landed on a dangerous flower, the foam covered pincers rapidly closed around the bee and trapped it for three seconds, after which the bee was released, mimicking an unsuccessful predatory attack by a crab spider (Thomisidae) (Ings and Chittka, 2008).

Aside from flower colour, there were no other cues available to the bee to indicate it was landing on a dangerous flower, paralleling a situation where predators are

camouflaged or visually undetectable. When subjects landed on a safe flower, no pinching occurred and bees were free to feed. After subjects returned to the hive to offload sucrose solution, the positions of the dangerous and safe flowers were changed so the spatial locations of the flowers could not be learned. Subjects were trained with this paradigm for a minimum of 100 flower landings.

(d) Tests: Behaviour in safe versus dangerous environments

Straight after the training period, bees were presented with a predation-free setting, but one set of bees was faced with the flowers of the colour associated with danger during training, while another group was presented with the ‘safe’ colour. Bees from the three colonies were randomly allocated to the two treatments. Before releasing the test bee into the arena, we randomly selected one of the eight flowers and allowed three nestmates (hereafter referred to as ‘demonstrators’) to feed from this flower only. To facilitate the demonstrators to feed from this flower exclusively, we trained them to feed from the selected flower prior to the start of experiments. Moreover, we increased the volume of sucrose solution provided by the flower (from 5 μ l to 1ml of sucrose solution) to ensure demonstrators remained on the flower for the duration of the test. Once all three bees had started feeding on the selected flower, the remaining seven flowers were also rewarded with the same quantities. When the demonstrators were in place, the test bee, which was being held in the tunnel connecting the arena and nestbox, was released into the flight arena and its first flower choice (i.e. the first flower it landed on) was recorded.

(e) Control: effects of predation risk or reduced rewards?

Visits to ‘dangerous’ flowers entailed a reduced reward as well as a simulated predator attack. This parallels the natural situation where a spider will typically attack before a bee finishes feeding. However, this means that subsequent changes in behaviour could be attributed to receiving smaller quantities of nectar rewards due to interruption by predators. To tease apart whether changes in behaviour in subsequent tests occurred as a result of predation or reduced reward, we tested a further control group of 14 bees from a different colony on dangerous flowers in the test phase. In this group, bees were not exposed to simulated predation attempts *during* feeding, but were allowed to complete feeding on the flowers associated with danger before being attacked. All other aspects of training were identical in this ‘post-reward predation control group’.

(e) Analyses

To confirm whether subjects in all treatment groups learned to associate the respective flower colours with safety and danger, we compared the proportion of landings on the safe flowers, made in the last ten choices of the training phase, with chance expectations (0.625), using a two-tailed binomial test.

To establish whether bees would preferentially land on the flower hosting the three demonstrators in the test phase, we then compared the proportion of bees that chose the nestmate occupied flower against chance expectations (0.125), again calculated using a two-tailed binomial test. To ascertain whether landing choices varied according to the test environment (safe or dangerous), flower colour or training

performance (the proportion of correct choices made in the last ten landings of the training phase), we performed a Generalized Linear Model with a binomial error distribution on data from the two main treatment groups, fitting all factors as predictors. We sequentially dropped non-significant terms until further simplification resulted in a significant decrease in explanatory power of the model, evaluated using chi-squared tests.

If the demonstrators finished feeding before the test subject had made a flower landing we excluded that test bee from our analyses. This left us with the following sample sizes: bees tested with the safe flowers: $n=14$; bees tested with the dangerous flowers: $n=14$; post-predation reward bees tested with dangerous flowers: $n=10$. All analyses were carried out using R statistical software (v.2.12.0).

6.4 Results

Bees in all treatment groups were highly successful in learning to associate flower colours with safety and danger in the training phase, choosing the safe flowers significantly more than expected by chance, assessed from the last ten landings in the training phase (mean performance \pm SD: bees tested on flowers previously associated with safety, $99.3 \pm 2.7\%$, two-tailed binomial test $p < 0.001$; bees tested on flowers previously associated with danger, $98.6 \pm 3.6\%$, $p < 0.001$; post-predation reward control group, $100 \pm 0\%$, $p < 0.001$).

We found that the testing environment (whether bees foraged among flowers linked to safety or danger in the previous phase) had a significant effect on whether bees joined conspecifics or not ($\chi^2 = 7.79$, d.f. = 1, $p < 0.01$). When test subjects were

presented with the flower colour associated with danger, there was a significant preference to land on the flower with feeding nestmates (figure 5.2; two-tailed binomial test: $p < 0.001$). Most of these subjects displayed hesitation by hovering in front of each unoccupied flower for a few seconds before rejecting it and moving onto the next until they encountered a flower occupied by nestmates where they landed and fed. However, when bees were presented with the 'safe flowers', subjects generally showed no hesitation and landed on the first flower they came across regardless of whether it was occupied by other bees or not. In this treatment group, only two of the 14 bees landed on the flower occupied by conspecifics, which is entirely in line with chance expectation (figure 5.2; two-tailed binomial test: $p = 0.692$) demonstrating that bees in this situation ignored social information and chose to land on flowers at random spatial positions when they had learnt that this particular flower colour was not associated with danger. Flower colour ($\chi^2 = 1.88$, d.f. = 1, $p = 0.17$) and training performance ($\chi^2 = 0.4$, d.f. = 1, $p = 0.53$) had no significant effect on the landing choices of bees.

When bees received equal amounts of sucrose solution on dangerous and safe flowers in the training phase, subjects still significantly preferred to join the flower occupied by other conspecifics when confronted with 'dangerous flowers' (figure 5.2; two-tailed binomial test: $p < 0.001$), suggesting that joining behaviour occurs solely in response to danger and is not a result of receiving less sucrose solution on flowers associated with danger.

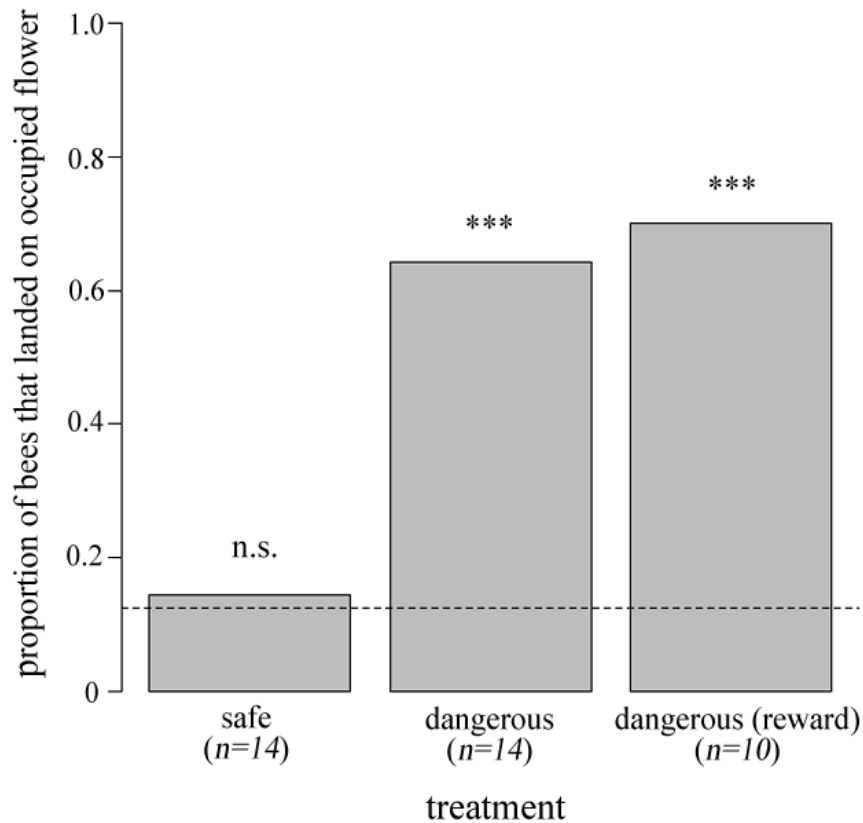


Figure 6.2 Proportion of bees, in the various treatment groups, that landed on the occupied flower in the test phase. The key comparison is illustrated with the left two columns where bees were presented with the flower colour previously associated with safety and danger respectively. Bees foraging in a safe environment showed no propensity for joining conspecifics, while bees foraging on flowers with a colour previously associated with danger strongly preferred occupied flowers. Subjects in the control group (dangerous (reward)) had been allowed to complete feeding on dangerous flowers during training. Chance expectation of visiting the occupied flower is indicated by the dashed line. n.s. denotes not statistically different from chance; *** denotes $p < 0.001$.

6.5 Discussion

Our findings clearly demonstrate that bumblebees choose to feed with other conspecifics when previous experience indicated that they were facing a perilous foraging situation. It is clear that this social information use occurs in response to danger alone, and is not a result of receiving less food because of an attack, since bees still chose to join conspecifics after they had been trained to learn that dangerous and safe flowers were equally rewarding. When no threat is detected, social information is ignored, demonstrating that bumblebees actively decide when to use social information according to the environmental context.

From a mechanistic perspective, the social foraging experience that all bees experienced in the pre-training phase may have led to the formation of positive associations with conspecifics, potentially explaining why bumblebees were attracted to nestmates under conditions of predation threat. However, subjects that were presented with the safe flowers had also previously foraged with conspecifics, yet showed no such attraction towards nestmates, suggesting that these associations manifest only under conditions where it is adaptive.

In nature, many flower species (particularly in the Asteraceae family) contain multiple nectaries, where the available nectar rewards are not immediately depleted by a single visitor and several pollinators can feed simultaneously (figure 5.3). This foraging scenario parallels the pre-training phase (which all social treatment groups experienced), where individuals had the opportunity to feed together with conspecifics in absence of competition. However, in the wild, other flower species are depleted by a single pollinating visitor, and in such a scenario, perhaps previous

competition with conspecifics could result in bees responding differently to social information in risky environments.

The behavioural strategy we observe here is consistent with existing social learning theory, which predicts that social information should only be used in specific fitness enhancing circumstances (Laland, 2004; Webster and Laland, 2008; Toelch et al., 2009). When information is not costly to acquire (such as landing at a flower where there is no predation risk), it is more beneficial to use personal information than to follow conspecifics. This is because, typically, more food resources are acquired by feeding alone than sharing the resource with multiple individuals. Conversely, when information acquisition imposes a high risk, like feeding on a flower potentially harbouring predators, it will be more beneficial to use social, rather than personal information, even if this carries a significant cost in food intake. For example, previous research demonstrates that bumblebees that encounter flowers with which they are already familiar, avoid flowers occupied by conspecifics, yet conversely seek out conspecifics when foraging from unfamiliar flowers, most likely in response to the costs involved with personal exploration, such as trial and error sampling (Leadbeater and Chittka, 2005; Kawaguchi et al., 2007). However, we should be cautious in placing our findings in a similar theoretical framework since competition between conspecifics for food was not a feature of this experiment, which could well render insignificant the usual trade-off between foraging efficiency and predation risk.



Figure 6.3. Multiple pollinators, of the same and different species, are often observed feeding together on inflorescences with many nectaries potentially leading to bees acquiring the social pre-foraging experience which facilitates joining behaviour in dangerous environments. (a) *Bombus terrestris* foragers feed from an ornamental thistle (*Cirsium rivulare*) (photo credit: Richard Burkmar, with permission). (b) *B. terrestris* and *B. pascuorum* individuals collect resources from a creeping thistle flower (*Cirsium arvense*) (photo credit: Stephan Wolf, with permission). (c) *B. terrestris* feed together on a globe thistle (*Echinops ritro*) (photo credit: Kiran Ravilious, with permission).

Previously it has been shown that the non-consumptive effects of predators (e.g. through avoiding flowers on which a predator attempt was made and subsequently all flowers of a similar appearance (Ings and Chittka, 2009)), can have significant influences on plant fitness and the dynamics of pollinator-plant interactions (Louda, 1982; Suttle, 2003; Gonçalves-Souza et al., 2008). However, our results suggest that such generalised avoidance behaviour might be counteracted to some extent by using social information since bees readily resumed foraging activity on flowers they previously perceived to be dangerous after joining conspecifics. Thus social information use may have profound and complex implications for pollination services.

In closing, this study adds to the body of evidence demonstrating the importance of social information in anti-predator behaviour by revealing a hitherto unknown social predator avoidance tactic in pollinators. Furthermore, our findings strengthen the observation that the use of social information is dictated by conditions in which they are most useful (Rendell et al., 2010) rather than following a hard-wired set of behavioural rules.

Chapter 7: General discussion and conclusions

7.1 Overview of chapters

In the last ten years, the opinions regarding the psychological mechanisms underlying social information use and learning have changed drastically. No longer is the ability to learn from others considered to stem from specialised adaptations, restricted to taxonomically higher-order animals; instead, it is postulated that animals, including insects, capable of learning individually, should be able to socially learn (Heyes, 1994; Leadbeater and Chittka, 2007b; Heyes, 2012). The general aim of this thesis has been to further explore this hypothesis. Using bumblebees (*Bombus terrestris*) and honeybees (*Apis mellifera*) as model systems, I have examined whether natural selection has shaped social learning processes, paying close attention to the underlying associative mechanisms and the role learnt and unlearnt predispositions play in social information use. In addition to this, I have explored whether social information is used adaptively or whether bees are completely inflexible in their approach. Overall, my findings suggest that while social learning processes derive from general associative mechanisms, enabling individuals to use social information in a flexible manner, evolution may still have modulated the ways in which bees process social information.

7.1.1 The role of general learning processes in social learning

Associative mechanisms have been implicated in facilitating social learning phenomena in many animals. The most straightforward scenario simply involves inadvertent social cues gaining biological relevance by being experienced in parallel with unconditioned stimuli, such as food or a predator attack (Leadbeater and Chittka, 2007b, 2009). Yet, many animals are capable of learning from others without forming these direct associations, suggesting that selection has favoured animals to treat stimuli from conspecifics as biologically important. In Chapter two we explored this idea by testing whether seemingly innate responses to conspecific behaviour could, in fact, also arise through associative learning. We found that bumblebees copied others only after conspecific presence had been reliably associated with food, highlighting that bumblebees are not predisposed to use social information; rather, conspecific behaviour gains relevance only through individual learning. While on first appearance, learning by observation may seem like a relatively complex cognitive process, we demonstrate a parsimonious associative learning mechanism that may account for many documented examples across the animal kingdom.

Yet, while we find that the underlying learning mechanisms which enable social learning and social information use may not be specially adapted, does this mean that selection has had no hand in shaping social information use? Animals may be adapted for receiving information from other agents, either through motivational or perceptual systems, resulting in a higher likelihood of forming associations with conspecific cues over alternative stimuli (Heyes, 2012; Lotem and Halpern, 2012). This was the focus of Chapter three, in which I investigated how bumblebees

differentially learnt to use a variety of social and non-social cues. Bees were undiscerning when it came to learning from conspecific and heterospecific social cues, yet when required to learn non-social cues in an identical paradigm, learning performance decreased significantly. Could this result reflect genetic predispositions for learning social cues over non-social alternatives? Perhaps; after all, bees are required to recognise a variety of social cues for purposes other than foraging. But as Heyes (2012) highlights, biases for using social information could also arise through experience. For example, bumblebees develop and reside in a colony with many other nestmates presenting an opportune chance for learning conspecific scents, especially if experienced together with food. An interesting future avenue of research would be to carry out comparative social learning studies between phylogenetically related social and solitary species that share the same ecological niche. Fundamentally, establishing innate predispositions towards social information use lies at the heart of understanding its evolution and further work is required to address these questions.

Clearly there are instances where evolution has shaped the use of social information, evident by the number of social signals that are present across the animal kingdom. Most animals display a stereotyped response to these signals, but can they also play a role in learning? In Chapter five, we explored this question by investigating whether honeybees could learn to avoid an asocial stimulus by associating it with a social signal. Many studies have demonstrated that different animals are able to acquire a fear response to new predators by experiencing them in conjunction with conspecific alarm signals (Mineka et al., 1984; Cook et al., 1985; Mineka and Cook, 1988, 1993; Chivers and Smith, 1994b; Wisenden et al., 1997; Chivers and Smith, 1998; Mirza

and Chivers, 2002; Griffin, 2004). However, in all of these studies (but see (Curio et al., 1978; Chivers and Smith, 1994a)) it is unclear whether predator cues are specifically being learnt or whether exposure to predator cues simply cause animals to react fearfully to all subsequent encountered stimuli (Griffin, 2004). Our study took this ambiguity into account and unequivocally showed that through Pavlovian conditioning, honeybees are able to associate an asocial stimulus with social alarm cues to acquire a fear response. Overall, I highlight general associative mechanisms underlie learning from both inadvertent social cues and specialised social signals.

7.1.2 A flexible approach to using social information

Clearly animals have evolved to respond to social signals in specific circumstances. For example, in situations of a predator threat to the hive, honeybees react to conspecific alarm cues by stinging and attacking the source of danger. But in scenarios where animals encounter social information produced unintentionally, does it always pay to use that information? Recent computer simulations suggest that a dominant social learning approach is the most successful strategy for acquiring fitness enhancing information (Rendell et al., 2010), yet this strategy does not always reflect empirically documented behavioural patterns. Even communicative social signals, which are used to elicit stereotyped behaviours in the receiver, are shown to be used selectively (Wray et al., 2012; Grüter et al., 2013). Animals are known to employ a number of different strategies when using social information, such as ‘copy when asocial learning is costly’ or ‘copy successful individuals’ (Templeton and Giraldeau, 1996; Laland, 2004; Saleh et al., 2006; Mery et al., 2009). In this thesis, I

demonstrate that bumblebees also use social information discerningly. In Chapter four, I found that wild bees used social information depending on whether they were foraging from familiar or (potentially) unfamiliar flowers, and in Chapter six, it was shown that bumblebees only joined conspecifics when information was dangerous to acquire.

Are these strategies genetically inherited or does learning influence when animals use, and learn from, social information? If information is consistently costly or hard to acquire, or responding to social cues in specific situations constantly and reliably results in an optimal behaviour, natural selection may select for genes which fix the circumstances in which animals should use social information or signals (Rendell et al., 2010; Reader, 2014). Some cases in the social learning literature show that animals still use social information even when it is suboptimal, suggesting a fixed strategy (Reader, 2014). For example, guppies (*Poecilia reticulata*) that socially learnt to take an energetically demanding route to food, persisted with the same route, even when an alternative, less costly route was provided (Laland and Williams, 1998). If social learning strategies are genetically encoded it would also unequivocally imply that the use of social information in animals does indeed arise through specialised adaptations selected for by evolution.

Alternatively, past experience could lead animals to learn when and when not to use social information. For example, individuals may be more likely to form associations with social cues if there is a higher number of exposures, following a ‘copy the majority’ strategy, or if social cues result in a visible reward, following a ‘copy the most successful’ strategy (Heyes, 2012). This learning hypothesis is supported by the numerous studies which demonstrate that early experience is integral to whether

animals use a social learning strategy or not. For example, house sparrows (*Passer domesticus*) reared with a parent that consistently provided information about food were more likely to use social information in future foraging expeditions, while those reared with a parent that inconsistently indicated food were more likely to later rely on their own explorations (Katsnelson et al., 2008). A similar finding emerged from Chapter two where it was shown bees only used social cues after experience led them to use them as a reliable source of information.

Learning these strategies enables animals to use social information flexibly, rather than being constrained to a hard-wired set of rules, which may become redundant when conditions change. But this then raises the question of just how flexible learnt strategies are. Would an animal apply the same learnt rules of thumb to situations involving heterospecific species? Also, would individuals generalise these rules across different circumstances (Grüter and Leadbeater, 2014)? For example, if a bird learns to copy successful individuals when choosing a nest site (Seppänen et al., 2011), would successful individuals still be followed when foraging for food or avoiding predators? Furthermore, animals may be confronted with situations where several strategies are possible. For example, an animal could have the option of copying the majority, but the minority are more successful. In such scenarios do animals prioritise strategies? Answering these questions could additionally give us greater insights into the evolution of social information use.

7.2 Conclusion

What makes social learning ‘social’? This question has been the central theme to this thesis in which I have explored the proximate mechanisms mediating social learning and the adaptive manner in which bees use social information. Taken as a whole, the work presented and reviewed here illustrates that animals may be specially adapted for receiving and responding to social information, through processes selected for by evolution, but, ultimately, the mechanisms which enable individuals to learn from this information are the same as those which facilitate general learning. Therefore, providing that animals are equipped with the ability to form associations between stimuli, it follows that they should also be able to learn to use cues originating from other individuals.

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