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REVIEW

Mechanisms of social learning across species boundaries

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Abstract

Social learning involves the acquisition of information from other individuals and is a behavioural strategy found in a wide range of taxa from insects to humans. Traditionally, research in this field has concentrated on learning from members of the same species; however, there is increasing evidence for social learning across species boundaries. Owing to the ecological overlap of many species, it makes sense that such heterospecific social learning is common, and in some cases, information from another species may be more profitable than that provided by members of the same species. Here, we review the existing literature about learning from individuals of different species. We discuss the cognitive mechanisms underlying this form of information gathering and highlight the importance of past experience and innate predispositions in the formation of interspecific learning events. In many cases, seemingly complex forms of 'copying' from members of other species can be explained by relatively simple forms of conditioning.

> I saw several humble-bees . . . visiting these flowers . . . cutting with their mandibles holes through the under side of the calyx and thus sucking the nectar . . . and the humble-bees were thus saved much trouble in sucking. The very next day I found all the hive-bees, without exception, sucking through the holes which had been made by the humblebees . . . I must think that the hive-bees either saw the humble-bees cutting the holes and understood what they were doing and immediately profited by their labour; or that they merely imitated the humble-bees after they cut the holes . . .' Charles Darwin quoted in Romanes (1883, pp. 220–221)
> '. . . should this be verified, it will . . . be a very instructive case of acquired knowledge in insects. We should be astonished did one genus of monkeys adopt from another a particular manner of opening hard-shelled fruit; how much more so ought we to be in a tribe of insects . . . so pre-eminent for their instinctive faculties, which are generally supposed to be in inverse ratio to the intellectual!' Charles Darwin (1841, p. 301)

Introduction

Animals are surrounded by a variable and complex environment in which they have to exhibit the appropriate behaviour to succeed in getting food, finding the best habitat or avoiding predation. Animals often share the same needs and problems with other individuals. Thus, in addition to gathering information personally by costly trial-and-error strategies, an individual can rely on information previously sampled by conspecifics regarding the quality of alternatives when deciding from what and where to feed, where to live or from whom to escape (Danchin *et al*., 2004; Galef & Laland, 2005; Grüter, Leadbeater & Ratnieks, 2010). Such social learning is widespread in the animal kingdom, from insects to mammals (Freeberg, 2000; Galef & Giraldeau, 2001; Brown & Laland, 2003; Leadbeater & Chittka, 2007). It can be defined as the use of social cues, often inadvertently left by other animals engaged in making choices between various options (Heyes, 1994; Danchin *et al*., 2004; Dall *et al*., 2005; Leadbeater & Chittka, 2007).

However, the use of socially acquired information should be regulated by adaptive strategies concerning when to copy and from whom (Laland, 2004). A rigid preference for social learning over personal sampling can lead to suboptimal choices: when the percentage of individuals gathering personal information is too low, this can result in informational cascades, where animals 'blindly' follow each other's choices without updating information about alternatives (Giraldeau, Valone & Templeton, 2002; Rieucau & Giraldeau, 2011). In addition, competition among individuals within a group can be increased by overexploitation of the same resources, even if novel, potentially more profitable resources might be available. In this context, monitoring the food choices of individuals of other species can be a rewarding strategy. Information provided by selected heterospecifics that share similar food sources, habitats or predators could be as valuable as information gathered from conspecifics (Fig. 1). Heterospecific animals may differ in their vigilance levels, perceptual capacities or information gathering methods (Raine *et al*., 2006; Goodale *et al*., 2010). Thus, relying on heterospecifics can provide access to information that is difficult to obtain by individual sampling and indeed from conspecifics (Chittka & Leadbeater, 2005). Furthermore, while acquiring information from conspecifics can increase competition for resources, such competition might be less pronounced if information is obtained from heterospecifics whose demands only partially overlap (Seppänen *et al*., 2007).

From the perspective of learning psychology, social learning across species boundaries is likely to be widespread. It has been suggested that social learning relies not on distinct cognitive modules shaped by evolution under social conditions, but instead hinges, at least partially, on the same mechanisms as individual learning (Heyes, 1994, 2011; Shettleworth, 1998; Galef & Giraldeau, 2001; Leadbeater & Chittka, 2007; Zentall, 2012). For example, social learning is observed in non-social organisms and individual variation of social learning performance within species co-varies with individual learning performance (Heyes, 2011). In this view, conspecific behaviour provides just one of the many types of conditioned stimuli that can be used to predict environmental contingencies (Chittka & Leadbeater, 2005). This being so, there is no reason to assume that animals might not be equally ready to use cues emitted by heterospecifics, if these reliably predict reward or punishment. If animals can at all assess the usefulness of a model for deciding whom to copy (Laland, 2004), then the model might with some probability belong to a different species. That is not to say that species membership of models in social learning is necessarily arbitrary. After all, most animals can recognize members of their own species for purposes other than social learning, and they might therefore possess sensory filters ('templates') or cognitive processes that attach special weighing to stimuli emanated by conspecifics, as, for example, in bird song learning (Marler, 1970; Konishi, 1985). In this review, we present the current evidence in various behavioural domains of heterospecific social learning and discuss the potential underlying mechanisms.

Predator recognition

Avoiding predators is one of the most crucial challenges that animals face. However, animals have to deal with a trade-off between time spent being vigilant versus other activities such as foraging or mating (Ings & Chittka, 2008). Living in a group provides advantages by increasing the number of sensors available for predator detection, but it also enables animals to learn from knowledgeable individuals to recognize predators (Griffin, 2004; Bell *et al*., 2009). Even non-social animals can benefit from the surrounding vigilant heterospecific animals sharing the same habitat to improve their detection rate (Fig. 1). Furthermore, the overall detection probability can be increased because of species differences in

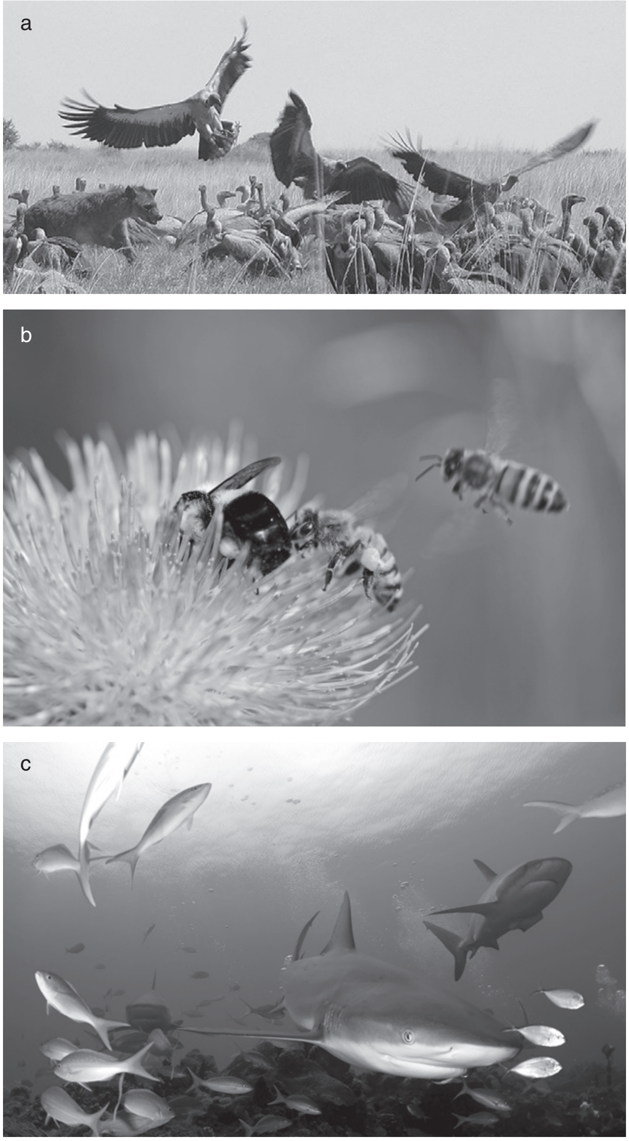

Figure 1 Using cues from heterospecifics can be ecologically adaptive. (a) A hyena *Crocuta crocuta* and vultures feeding from the same dead zebra (photo credit: Matthew Westercamp, with permission). Vultures circling above prey provide a valuable distant indicator of scattered food sources for hyenas. (b) A bumblebee (*Bombus impatiens*) and honeybees (*Apis mellifera*) on the same flower (photo credit: Shelly Cox, with permission). Pollinators searching for flowers might often encounter same-species as well as different-species flower visitors whose activities can equally indicate flower profitability. Many flower species are often present together in a habitat but can differ by more than an order of magnitude in terms of their nectar contents. Monitoring other pollinators' activity might be a rewarding strategy to decide which flowers to sample. (c) Sharks (*Carcharhinus perezi*) visiting a coral reef (photo credit: Willy Volk, with permission). Coral reefs are habitats for many different fish species that are predated by the same shark species. Reacting to the escape behaviour of other fish instead of relying only on one's own survey of the surrounding environment can reduce predation risk.

terms of perceptual sensitivity or vigilance. Thus, 'eavesdropping' on alarm cues generated by heterospecific animals is often a rewarding strategy.

Reactivity to heterospecific alarm cues (e.g. alarm calls, fleeing movements and chemical cues) has been found between fish species (Brown, 2003; Pollock *et al*., 2003), different species of frogs (Phelps, Rand & Ryan, 2007), birds (Griffin *et al*., 2005; Templeton & Greene, 2007; Magrath, Pitcher & Gardner, 2009*a*,*b*; Magrath & Bennett, 2012) and lemur primates (Fichtel, 2008). Moreover, this information transfer also occurs across widely different taxa such as between Galápagos marine iguanas and mockingbirds (Vitousek *et al*., 2007), red squirrels and jays (Randler, 2006), dik-dik ungulates and go-away birds (Lea *et al*., 2008), Diana monkeys and hornbill birds (Rainey, Zuberbühler & Slater, 2004), and between impala ungulates and baboons (Kitchen *et al*., 2010).

A few species are known to emit different alarm calls depending on the nature of the threat (e.g. Seyfarth, Cheney & Marler, 1980; Slobodchikoff *et al*., 1991; Manser, Seyfarth & Cheney, 2002; Seyfarth & Cheney, 2003), and some animals are capable of responding appropriately to the specific message of the alarm code used by another species. For example, white-browed scrub wrens (Leavesley & Magrath, 2005) and superb fairy-wrens (Fallow & Magrath, 2010) both add more elements to their alarm call when the predator distance decreases, thus coding the emergency of the threat. Fallow & Magrath (2010) showed that both species responded to each other's alarm code in accordance with the encoded message: the birds are more likely to flee and stay under cover for longer when hearing heterospecific playbacks that include more elements. Similarly, black-capped chickadees can specify information about the associated risk and size of the predator in their call (Templeton, Greene & Davis, 2005). Red-breasted nuthatches show the appropriate reaction when hearing the chickadees' alarm calls (Templeton & Greene, 2007). Among primates, Diana monkeys produce different types of alarm calls depending on whether the predator is an eagle or leopard (Zuberbühler, Noë & Seyfarth, 1997). Hornbill birds, sharing the same habitat, are also predated by eagles but not by leopards and therefore respond only to eagle-specific Diana monkey alarm calls despite the similarity between both types of calls (Rainey *et al*., 2004; Fig. 2a). In addition, Diana monkeys are sensitive to the semantic content of the alarm call of Campbell monkeys, which also provides information about the nature of the threat (Zuberbühler, 2000).

Inadvertent information provided by heterospecific individuals detecting a predator threat may also be used to learn to identify an unknown animal as a threat. Woodfrog tadpoles can learn about the danger associated with salamanders by experiencing the anti-predator behaviour (decrease of activity) towards salamander chemical cues of knowledgeable heterospecific tadpoles (of boreal chorus frogs) in mixed-species assemblages (Ferrari & Chivers, 2008).

Impressive though they may seem, many if not most of these 'interpretations' of heterospecific alarm cues have simple mechanistic explanations. In some cases, closely related species may simply respond to heterospecific calls that have similar acoustic properties to their own calls (de Kort & ten Cate, 2001; Fallow, Gardner & Magrath, 2011). A study on pipistrelle bats located in England and Northern Ireland found that three sympatric species all responded to each other's distress calls – yet when one species of the bats was exposed to the distress calls of geographically isolated bats, endemic to Madagascar, there was also a significant response. Analysis of the distress calls revealed apparent acoustic similarities in call structure between the different bat species (Russ, 2004). It is also likely that in the previous example with tadpoles, both tadpole species (boreal chorus frog and woodfrog) share a similar anti-predator behaviour or an alarm pheromone, thus explaining the direct association between the salamander cue and the natural unconditioned stimulus of the anti-predator behaviour. Even where such cross-species similarities in alarm calls do not exist, responses to heterospecific signals can often be explained by basic forms of classical conditioning, where an unconditioned stimulus (predator appearance) is reliably predicted by an arbitrary conditioned stimulus (e.g. the alarm call of another animal). If a sympatric species' alarm call consistently predicts the presence of a generalist predator, then an association can be made between the alarm calls and a direct or indirect experience with that predator (Rainey *et al*., 2004; Fig. 2a). In free-living golden-mantled ground squirrels, it was found that a neutral sound, unrelated to any sympatric species, can be associated with the appearance of a predator (Shriner, 1999). This results in the (previously) neutral sound inducing an anti-predator response in the squirrels. Appropriate responses to other species' alarm calls must of course be preceded by a learning phase, during which a reliable correlation between particular cues and a predator threat is established (Hauser, 1988; Pollock *et al*., 2003; Fichtel, 2008). For example, Magrath & Bennett (2012) demonstrated that superb fairy-wrens react to noisy miner alarm calls only at sites where noisy miners are present, suggesting increased opportunities for learning the relevant associations (see also Brown, 2003; Diego-Rasilla & Luengo, 2004; Phelps *et al*., 2007; Magrath *et al*., 2009*b*). Similarly, impalas share significant spatial overlap and predation risks with baboons, and indeed impalas display the strongest and most accurate response to baboon alarm calls in comparison with three other ungulate species (Kitchen *et al*., 2010).

Food source location

Location of profitable food sources is crucial for an animal's survival. Relying on other individuals' search behaviour, in addition to one's own, can save time and energy (Fig. 1). Although conspecific attractiveness in foraging behaviours is well documented (Galef & Giraldeau, 2001; Leadbeater & Chittka, 2007; Grüter *et al*., 2010), less is known about social learning between species when searching for food. Yet, several species often share similar food sources, which can lead to mixed-species assemblages (Goodale *et al*., 2010), for example, multiple sympatric pollinator species often visit the same flower species (Waser *et al*., 1996; Fig. 1). Therefore, heterospecifics' foraging activities may be just as reliable as conspecifics in locating a profitable source (e.g. Rubenstein *et al*., 1977; Carlier & Lefebvre, 1997; Lefebvre *et al*., 1997).

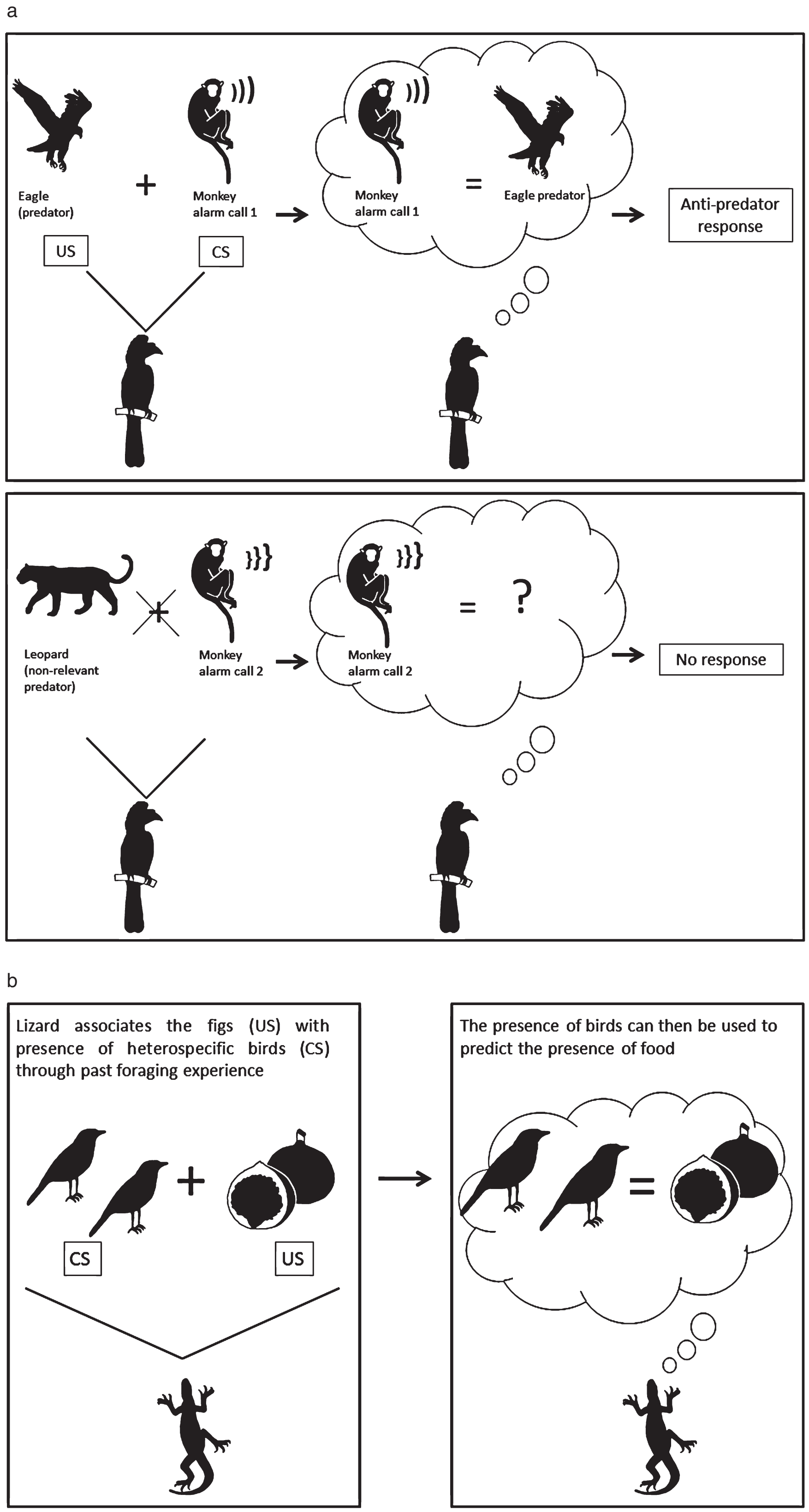

Figure 2 Heterospecific social learning through simple conditioning. (a) The association between the Diana monkey alarm call (conditioned stimulus) and the presence of a dangerous predator (a raptor – unconditioned stimulus) can lead the hornbills to predict the presence of the predator from the alarm call itself (anti-predator behaviour). By contrast, the specific alarm call emitted by Diana monkeys in the presence of a leopard does not induce an anti-predator response. The leopard is not a threat for hornbills (neutral stimulus) so no aversive association can be created with the alarm call (neutral stimulus). (b) Through simultaneous feeding with birds, the flat lizard can associate the occurrence of birds (conditioned stimulus) with the presence of food (unconditioned stimulus). This results in the lizard using the birds' presence as a predictor of fruit bearing trees.

Indeed, some well-documented examples of cross-species social learning occur in pollinators (Fig. 1). Dawson & Chittka (2012) demonstrated that bumblebees can learn to use the presence of heterospecifics to the same degree as conspecific information as an indicator of rewarding flowers through a simple associative learning mechanism. Interestingly, it was found that non-social cues were not as efficient as cues provided by other animals, suggesting that bumblebees have some form of predisposition to learning social cues (whatever the demonstrator species) over arbitrary visual cues.

Some stingless bees deposit chemical trails to transfer information about flower location to their nest mates. Foragers of the aggressive *Trigona spinipes* species can detect and use the odour marks left by foragers of another meliponine species, *Melipona rufiventris*, to orient themselves towards a novel food source and drive away or kill *M. rufiventris* foragers to efficiently exploit it. *Trigona spinipes* odour marks are repellent for *M. rufiventris* bees (Nieh *et al*., 2004), indicating that there may be an innate predisposition in the way heterospecific cues are used, depending on each species' competitive abilities.

Heterospecific cues can also be used to discern a depleted food patch via simple associations. It has been found that bumblebee foragers will actively avoid flowers that have been recently visited by using scent marks left by conspecific and heterospecific visitors (Goulson, Hawson & Stout, 1998; Stout & Goulson, 2001; Reader *et al*., 2005). However, if bees have no previous experience with these scent marks, they show no avoidance of flowers with such marks (Leadbeater & Chittka, 2011) and in fact, if a scent mark is coupled with a reward, as opposed to the absence of a reward, bees will seek out flowers with scent marks (Saleh & Chittka, 2006).

The dance language of honeybees, where successful foragers indicate to nest mates the distance and direction of a useful food source, is perhaps one of the most remarkable cases of social learning in the animal kingdom. 'Recruits' attend the figure 8-shaped dance routines by following the dancer in close contact, and subsequently decode the information from the dances and apply them in spatial and temporal removal from the act of picking it up, when flying to the indicated food source. A study on heterospecific social learning between two different species of honeybees, *Apis mellifera* and *Apis cerana*, revealed that the interpretation of the dance by recruits is less behaviourally hard-wired than originally thought (Su *et al*., 2008). These two species differ in their distance code so that the same food source is indicated subtly differently by dancers of the two species. When placed together in the same hive, however, *A. cerana* can learn to decode the dance 'dialect' of *A. mellifera*, presumably by a form of trial-and-error learning. They must first notice that their initially erroneous reading of the dances leads them to a reward-less location. When a subsequent search takes them to the rewarded site, a recalibration of their reading of the distance code apparently takes place, so that they subsequently read the 'foreign dialect' correctly.

The adaptive interpretation of heterospecific cues in foraging decisions is not limited to pollinators. South African Augrabies flat lizards often feed on energetically rich fig tree fruits and can travel considerable distances to find a fruiting tree. In this context, being able to access remote information about the ripeness of fruits is crucial. Whiting & Greeff (1999) showed that lizards can use birds' activity in the trees as a cue of fruit availability or ripeness (Fig. 2b). Furthermore, the lizards are attracted by experimentally manipulated bird congregations in trees as opposed to other fig trees containing only empty cages (Fig. 2b). Again, this attraction to heterospecific birds most likely results from simple Pavlovian conditioning. The lizards may have formed a simple association between the rewarding fruits (unconditioned stimulus) and the presence of the flocking birds (conditioned stimulus), thus explaining why the presence of the birds alone, without the fruiting trees, is enough to attract the lizards (Whiting & Greeff, 1999; Fig. 2b).

Examples where individuals learn from others (of the same species or a different one) by distal observation are not as readily explained by simple associative learning because there is no reward involved at the time of the observation. No direct association can therefore be established between the reward and the heterospecific cue. However, second-order conditioning could explain cases of learning by observation, whereby an individual learns to make the indirect association between a stimulus (second-order conditioned stimulus) and a reward (unconditioned stimulus) through observing other individuals interacting with this stimulus (Pavlov, 1927). In this scenario, prior association of other individuals (first-order conditioned stimulus) with the food reward is necessary. As an example, nine-spined sticklebacks were shown to correctly choose the spatial position associated with food in a dual-choice set-up after having observed three-spined sticklebacks eating in the same spatial position versus three-spined sticklebacks without food in another spatial position. These fish were also capable of choosing the appropriate spatial position after observing three-spined sticklebacks feeding in low-quantity versus high-quantity food conditions (Coolen *et al*., 2003). In this example, the cues marking the spatial position might be the second-order conditioned stimulus, while the food reward is the unconditioned stimulus (hidden from view of the tested fish) and the feeding behaviour of observed fish are the first-order conditioned stimuli (Fig. 3). Although yet to be formally tested, this rationalization could explain many cases of social learning where there is no direct reward provided to the observer at the time of viewing a heterospecific's feeding behaviour.

Choice of habitat/nest site

Another important function of heterospecific social learning involves the choice of a novel nest site or habitat. Having access to information about site quality from settled individuals can save the cost of extensive individual sampling of available options. It can be predicted that the occurrence of heterospecific social learning of habitat selection should be most evident in migratory animals. These animals face the challenge of rapidly finding a breeding site to allow enough time for their offspring to develop before the next migration. Therefore, obtaining cues about site quality from resident animals may provide a beneficial shortcut to increasing an individual's fitness.

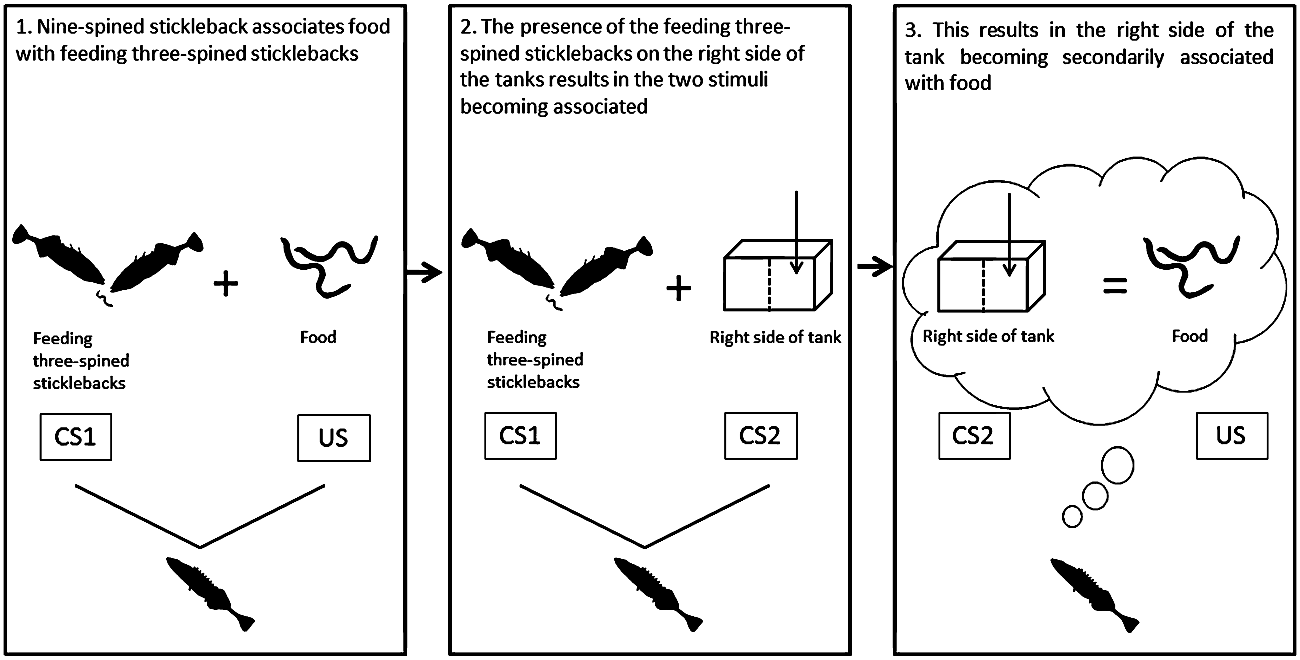

Figure 3 Heterospecific social learning resulting from a potential second-order conditioning process. Nine-spined sticklebacks can learn from observing heterospecific individuals' feeding behaviour in which tank compartment to find food. This behaviour could emerge from an integration of simple associations known as second-order conditioning. The heterospecific's feeding behaviour (first-order conditioned stimulus) was previously associated with food presence (unconditioned stimulus) in mixed-species feeding groups. Consequently, the spatial cues identifying the location of the compartment (second-order conditioned stimulus) becomes predictive of food presence by association with the first-order conditioned stimulus (heterospecific's feeding behaviour).

Studies on migrant passerine birds' nest site selection in northern boreal forests brought to light the importance of heterospecific cues in birds' decisions. When nest densities of resident tit species were experimentally manipulated in forest patches, therefore dissociating this density from any correlating factors such as the amount of prey available, a positive correlation was observed between the resident density and the number of novel settled migratory birds in a nearby area (Forsman *et al.*, 1998). Similar results were obtained in migratory chaffinches when the density of resident titmice nests was manipulated (Thomson, Forsman & Mönkkönen, 2003). Such interactions were also found between rollers and resident kestrels (Parejo, Danchin & Avilés, 2005). Additionally, flycatchers are able to learn arbitrary symbols placed on resident tits' nest sites and use them to make their choice between alternative options (Seppänen & Forsman, 2007). When the number of eggs in tit nests was experimentally manipulated, flycatchers were subsequently more attracted to the symbols associated with the more prolific nests when making their choices (Forsman & Seppänen, 2011; Seppänen *et al.*, 2011). Moreover, flycatcher females appear to adjust their own clutch size to that of their tit neighbours, thus using surveys from resident birds to gauge the richness of the habitat for raising their own offspring (Forsman, Seppänen & Nykänen, 2011).

Attractiveness of settled heterospecific animals was also observed in shrikes. These passerine birds adopt a raptor-like diet but without specific leg adaptations to dismember their prey. They consequently impale their prey to facilitate handling. Such larders are also used to mark a male's territory and as an indicator of male quality to conspecifics. These salient cues placed by great grey shrikes are also used by heterospecific red-backed shrikes as a reliable source of information about habitat profitability (Hromada *et al.*, 2008). In a completely different taxon, *Hypochilus thorelli* spiders appear to use the presence of existing webs of *Achaearanea tepidariorum* as an indicator of site quality as well as a support for their own webs (Hodge & Storfer-Isser, 1997).

As opposed to learning about predation threat and suitable food, it is slightly harder to put learning about habitat selection across species boundaries into the context of simple associative mechanisms. In such examples, 'observers' do not directly experience a reward such as food, or a negative stimulus, such as an empty foraging patch or a predator threat. A tentative second-order conditioning explanation could apply, whereby a positive association is formed between a rich habitat and heterospecific species presence, so that when the observer sees a bird select a particular nest site, the positive association is transferred to that particular site. However, such an association between a rich habitat and bird presence does not seem as direct as in mixed-species feeding examples. Instead, it appears that during the previous breeding season, the migrant birds must have surveyed the different potential sites and established a correlation between their quality and heterospecific presence, which would seem to be a remarkable case of latent learning, or indeed 'deliberate' reconnaissance. Further research is required to uncover the mechanisms behind this kind of impressive interspecific information use.

Heterospecific information use between humans and other animals

Special cases of heterospecific social learning occur in the collaboration between humans and domestic animals. While some might question the biological relevance of these processes, such information transfer is nonetheless informative about potentially more cognitively demanding forms of social learning, including imitation. If animals are in principle capable of sophisticated learning from humans, then it seems plausible that these forms of information transfer can also potentially occur between different species of wild animals, so that one might observe, for example, that 'one genus of monkeys adopt[s] from another a particular manner of opening hard-shelled fruit' (Darwin, 1841; Romanes, 1883).

The 'understanding' of the human pointing gesture has been particularly well studied (Miklósi & Soproni, 2006). Typically, tested animals have to select an item pointed at by a human experimenter, from a set of numerous items. It is clear that both a history of domestication, as well as an extensive interaction with human carers during ontogeny, might serve to equip subjects with the necessary skills (Miklósi & Soproni, 2006). Indeed, bonobos and orangutans raised in captivity use pointing gestures to inform humans (Zimmermann *et al*., 2009), even though apes do not appear to use pointing gestures in the wild. Dolphins use rostrum pointing naturally themselves (Pack & Herman, 2006; Pack & Herman, 2007), probably as a derivative of echolocation behaviour, and it is likely that their ability to interpret human pointing simply co-opts this natural behaviour with a heterospecific demonstrator. Many domesticated mammals, including dogs (Bräuer *et al*., 2006; Kubinyi, Pongrácz & Miklósi, 2009; Udell, Dorey & Wynne, 2010) and goats (Kaminski *et al*., 2005), can correctly interpret a variety of human pointing gestures even when the demonstrator stands relatively far from the pointed-at objects. Many other species, such as grey parrots (Giret *et al*., 2009), bats (Hall *et al*., 2011), horses (Maros, Gácsi & Miklósi, 2008), ravens (Schloegl, Kotrschal & Bugnyar, 2008), dingoes (Smith & Litchfield, 2010) and jackdaws (von Bayern & Emery, 2009), failed in distal conditions but not in proximal conditions (where the demonstrator touches or is very close to the objects) (Miklósi & Soproni, 2006). In proximal conditions, the mechanism might be a simple association between human hands and food as the tested animals are all human-raised (Miklósi & Soproni, 2006). The correct interpretation of pointing at more distant targets undoubtedly also involves associative learning, but in this case, attentional processes and an understanding of other's mental states have also been discussed (Anderson, Montant & Schmitt, 1996; Povinelli & Giambrone, 1999). It is intriguing to speculate that the process of domestication might either explicitly or implicitly have selected for animals to attend to social cues from humans: this suggests that the readiness for heterospecific social learning might respond relatively swiftly to pertinent selection pressures. This flexibility may also explain many of the differences in propensities to learn from sympatric species in the wild.

Imitation of movement has also been observed across species boundaries (Huber *et al*., 2009). Imitation has mainly been studied within species, but chimpanzees and dogs, for example, appear to be successful at imitating human demonstrators (Huber *et al*., 2009; Whiten *et al*., 2009). In the 'do as I do' paradigm, animals are asked to imitate human movements. This ability appears cognitively demanding as the animal has to establish a correspondence between the visual human movement and its own motor response. However, it has been suggested that imitation can at least in part be based on associative learning processes, based on responses by mirror neurons (Iacoboni, 2009; de Waal & Ferrari, 2010). These neurons, described in primates and birds (Prather *et al*., 2008), not only fire for a particular movement performed by the animal (e.g. grasping an object) but also respond when observing another animal performing the same action (Rizzolatti & Craighero, 2004). Therefore, through experience, these neurons might establish a link between the observation of a movement and its own motor realization (Catmur, Walsh & Heyes, 2009). Domestication and prolonged experience with humans might therefore facilitate the stimulation of mirror neurons in dogs when observing humans' actions. Finally, many examples of copying, where an animal learns how to use a device by observation, are not cases of 'true' imitation as the exact same movements are not reproduced. Instead, these cases should be considered as emulation (Tomasello, 1996; Huber *et al*., 2009), whereby the tested animal simply learns which part of the device is associated with food by observation (associative learning) but is not necessarily paying attention to the conspecific's movements. The observation induces emulation towards the device, thus increasing the probability for the observer to find the appropriate action by a trial-and-error mechanism. Indeed, 'ghost' experiments, where the device is automatically opened in front of the tested animal, are often just as efficient in allowing successful subsequent manipulations (Huber *et al*., 2009).

Concluding remarks

Despite the near-exclusive focus of the social learning literature on information acquisition from conspecifics, we have seen that heterospecific information transfer is widespread and occurs in all the ecological and cognitive domains in which within-species social learning is also found. In ultimate terms, the fact that animals often use information from heterospecifics might be unsurprising. Information about water and food availability, food toxicity, predator threats, etc., will often be of relevance for more than one species, and animals would do well to use public information from members of other species. Indeed, Seppänen & Forsman (2007) and Goodale *et al*. (2010) made a convincing case that heterospecific social cues might sometimes be more useful than those provided by conspecifics. Evolved predispositions towards copying only certain forms of information, and only from specific species of 'demonstrators', might often play an important role. The finding that among related species, some are more likely than others to use heterospecific information (Coolen *et al*., 2003; Slaa, Wassenberg & Biesmeijer, 2003; Nieh *et al*., 2004; Magrath *et al*., 2009a; Goodale *et al*., 2010; Kitchen *et al*., 2010) supports the hypothesis that a particular selection pressure (i.e. high predation risk or necessity to establish a nest quickly) is necessary to promote heterospecific social learning.

Conversely, eavesdropping of information by competitive and dominant species might lead to a reduction of the conspicuousness of signals displayed by the informant species (Seppänen *et al*., 2007; Goodale *et al*., 2010). The evolution of communication about food location in social bees may be a good example of the potential influence of eavesdropping on the evolution of social learning: some stingless bee species use pheromone trails that are liable to be learnt by competitors that might subsequently monopolize the indicated food source. To avoid such information exploitation, a possible solution is to 'hide' the transfer of information inside the nest, as in honeybee dance communication (Nieh *et al*., 2004). Indeed, the intense level of competition between bee species in tropical habitats might have favoured the evolution of referential communication (Dornhaus & Chittka, 2004; Nieh *et al*., 2004). Similarly, the role of eavesdropping on evolution can be implicated in egg covering behaviour of tits before incubation, during the period of habitat selection (Seppänen & Forsman, 2007). On the contrary, signal conspicuousness should be increased when the informant species benefit from the information transfer (Seppänen & Forsman, 2007). For example, drongo (Ridley, Child & Bell, 2007) and hornbill birds (Goodale *et al*., 2010) make more alarm calls in the presence of other species as these birds feed on the insects that surround the attracted heterospecific individuals. On the proximate level, social learning relies largely on similar mechanisms as individual learning (Heyes, 2011). From this perspective, the use of social cues (provided by conspecifics or heterospecifics) simply forms part of the spectrum of extracting contingencies between environmental cues and biologically relevant events. There might be differences in the *weighting* that animals give to non-social, conspecific or heterospecific cues when learning about their environment. The neural mechanisms and computational processes underpinning these learning behaviours might in many cases be the same, although there may be differences in peripheral (sensory) filters, as well as central nervous 'templates' that mediate differential effectiveness of various social and non-social cues. Such filters can be acquired individually or over evolutionary time, and the outcome might in many cases be an interaction of both. The existence of pre-existing templates for conspecific cues might explain why even songbirds, with extensive flexibility in learning courtship songs, have a certain preference for what might credibly constitute a species-specific song, unless they interact extensively with heterospecific 'tutors', in which case they might adopt completely atypical (for their species) vocalizations (Marler, 1970; Baptista & Petrinovich, 1984; Konishi, 1985).

One of the authors of this review, in his pre-school years, attempted to levitate by flapping his arms after observing ducks in a park, and to increase his running speed by imitating the sound of a galloping horse. Neither of these produced impressive results, indicating to this author that birds and equines were not suitable role models for locomotion. However, the implication is that some animals might be relatively flexible in what other animals they 'copy', and subsequently evaluate the usefulness of the copied behaviour, or the usefulness of the particular model in general. The level of flexibility might be determined by sensory or perceptual filters, attention-related processes or motivation (Heyes, 2011). But so long as animals are equipped with mechanisms to extract contingencies between environmental cues and biologically relevant stimuli (and all animals are), it follows that they should be able to pick up these cues from other animals, including individuals of other species.

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