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Title: Social information use by predators : expanding the information ecology of prey defences

Year: 2022

Version: Published version

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Please cite the original version:

Hämäläinen, L., M. Rowland, H., Mappes, J., & Thorogood, R. (2022). Social information use by predators : expanding the information ecology of prey defences. Oikos, 2022(10), Article e08743. https://doi.org/10.1111/oik.08743

OIKOS

Forum

Social information use by predators: expanding the information ecology of prey defences

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Oikos
00: 1–15, 2021
doi: 10.1111/oik.08743

Subject Editor: Kenneth Schmidt
Editor-in-Chief: Dries Bonte
Accepted 10 November 2021

Social information use is well documented across the animal kingdom, but how it influences ecological and evolutionary processes is only just beginning to be investigated. Here we evaluate how social transmission may influence species interactions and potentially change or create novel selection pressures by focusing on predator–prey interactions, one of the best studied examples of species coevolution. There is extensive research into how prey can use social information to avoid predators, but little synthesis of how social transmission among predators can influence the outcome of different stages of predation. Here we review evidence that predators use social information during 1) encounter, 2) detection, 3) identification, 4) approach, 5) subjugation and 6) consumption. We use this predation sequence framework to evaluate the implications of social information use on current theoretical predictions about predator–prey dynamics, and find that social transmission has the potential to alter selection pressures for prey defences at each predation stage. This suggests that considering social interactions can help answer open questions about species coevolution, and also predict how populations and communities respond to rapid human-induced changes in the environment.

Keywords: antipredator defences, information ecology, predator–prey interactions, social information

To make adaptive decisions, animals must continuously gather information (Dall et al. 2005), either from direct interactions with their environment ('personal information'), or by observing the behaviour of other individuals ('social information'). Social information can come from signals that have evolved specifically for communication, as well as from cues that are provided inadvertently when individuals observe, or eavesdrop on, the behaviour of conspecifics or heterospecifics (Danchin et al. 2004). Social information use has been demonstrated in many different contexts across the animal kingdom, including foraging, mate choice and habitat selection (Danchin et al. 2004, Gil et al. 2018, Whitehead et al. 2019, Penndorf and Aplin 2020). This flow of

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information can shape social structures and determine how individuals interact with each other and the wider environment (Cantor et al. 2021). Social transmission, therefore, has the potential to relax or intensify selection, or generate novel selection pressures, including during species interactions (Thorogood and Davies 2012, Whitehead et al. 2019). Although considering social information use can help answer open questions about species coevolution and community dynamics (Thorogood and Davies 2012, Gil et al. 2018, Whitehead et al. 2019), there has been little synthesis evaluating how social information use can influence ecological and evolutionary dynamics within the context of species interactions (Cantor et al. 2021). Here we address this knowledge gap using predators and prey, a text-book example of coevolution.

The importance of social effects in predator–prey interactions was recognised already in early studies of socially foraging birds (Emlen 1952, Turner 1964, Morse 1970, Pulliam 1973, Powell 1974). Since then, there has been extensive research into how prey can use social information to avoid predators (reviewed in Brown 2003, Griffin 2004, Ferrari et al. 2010, Magrath et al. 2015), but there is also a growing set of studies on social behaviour of predators. Indeed, recent work suggests that social information transfer among predators can affect the frequency-dependent dynamics of prey defences, and resolve long-standing questions in evolutionary biology, such as the maintenance of aposematism (Thorogood et al. 2018). However, we still know little about these population- and community-level effects (Gil et al. 2018).

To gain a comprehensive view of how social information use by predators influences prey defences, it is essential to investigate how and when selection can operate (Sheriff et al. 2020). Although often thought of with respect to its end result, predation is a consequence of a sequence of decisions and interactions between predators and prey (Ruxton et al. 2018). The classic view of a predation event as described by Endler (1991) consists of: 1) encounter, 2) detection, 3) identification, 4) approach, 5) subjugation and 6) consumption, and this framework helps us to understand how and why different antipredator defences have evolved (Ruxton et al. 2018). How predators use social information to decide whether to continue a predation sequence can then be conceptualised using a statistical decision theory approach (McNamara and Houston 1980, Dall et al. 2005, Fig. 1) where predators are considered to have prior 'knowledge' of the outcome of different actions (genetically determined or based on previous experience, Iwasa et al. 1981, Olsson and Holmgren 1998, van Gils et al. 2003, Olsson and Brown 2006, Kawamori and Matsushima 2010, Norbury et al. 2021). To reduce uncertainty, predators gather personal and/or social information to update this prior knowledge and this then generates a posterior probability distribution of different outcomes (Dall et al. 2005, Fig. 1). How animals integrate information, however, also depends on the costs of gathering it relative to the value of acting without the additional information. For example, a predator may have previous experience that conspicuous prey are usually unpalatable (i.e. optimal action is to reject the prey), but social information gathered from observing others consuming similar prey might change this prior expectation towards assuming that the novel conspicuous prey item is palatable (i.e. optimal action would shift to attacking the prey). Combining this statistical decision theory approach with the predation sequence therefore provides a framework for analysing a predator's information use and behaviour, as well as its potential evolutionary consequences for prey.

Here we discuss the adaptive use of social information by predators in each of the predation stages (Fig. 2). Although predators can use several cues, including eavesdropping cues from prey (reviewed by Hughes et al. 2012), we focus on social information gathered from observing the behaviour of other predators. We review empirical evidence of social transmission at each predation stage, and discuss how social information can influence the fitness of both predators and prey to evaluate potential effects on predator–prey dynamics. While the predation sequence provides a useful framework for our review, different predation stages are not independent of each other and the distinction between them is often not clear. For example, predators can acquire social information at one stage and use it in their decision-making at another stage. As our aim is to consider how social information shapes selection on prey defences, we have classified the examples of social transmission to different predation stages based on the potential effects on prey defences operating at that particular stage (as described by Endler 1991). Some examples might, however, fit in several stages, and we have included them in sections where we find them most relevant. Because the number of experiments testing social transmission explicitly in the context of predator–prey interactions is still low, the emerging ideas we discuss are relatively novel. Therefore, many of our predictions are tentative, and the aim of our review is to identify prospective areas for future research. Finally, we discuss the potential implications for predators and prey in a rapidly changing world.

1. Encounter

The first stage of predation requires a predator to get sufficiently close to prey to detect it. However, prey abundances and distributions change over time and space, creating a complex, rapidly changing environment (Pyke et al. 1977). Efficient foraging decisions can be based on previous experience and individual search behaviour (Krebs 1973), but there is also extensive literature showing that animals use social information to locate high-quality food patches (Elgar 1986, Templeton and Giraldeau 1995, Laland and Williams 1997, Coolen et al. 2003, Clark 2007, Gillam 2007, Farine et al. 2015). This includes inadvertent information, such as visual or chemical cues, or echolocation calls to locate prey patches (Clark 2007, Gillam 2007), and signals that have evolved to recruit others to food sites (e.g. food calls and odour trails; Elgar 1986, Judd and Sherman 1996, Hillemann et al. 2019). However, the use of social

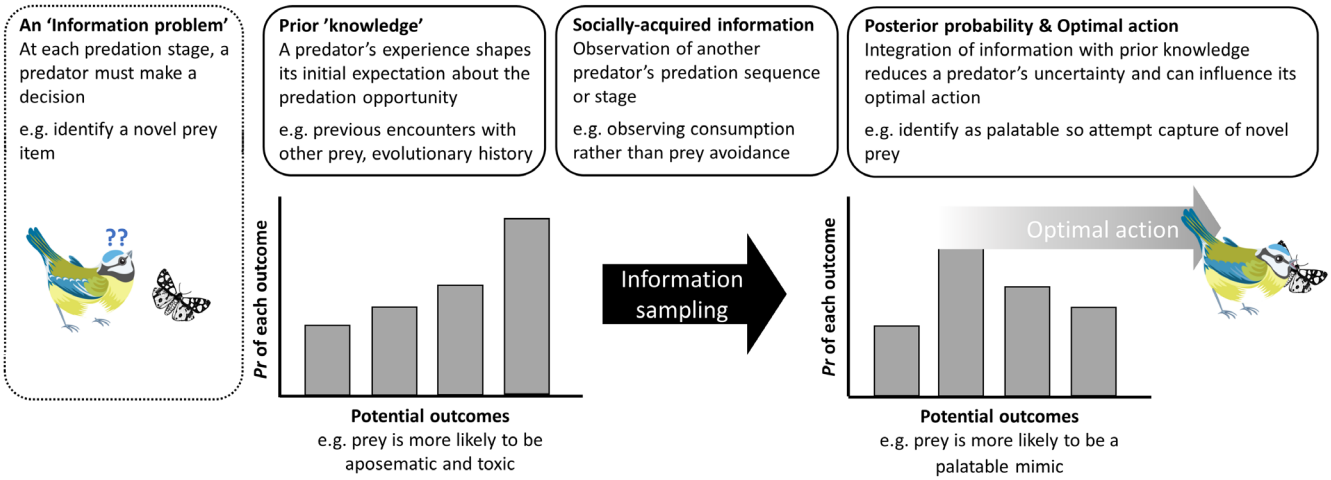

Figure 1. A statistical decision theory framework (Dall et al. 2005) can be used to describe and evaluate the adaptive use of social information by predators. During a predation sequence, a predator has prior 'knowledge' that determines the probability (*Pr*) of a range of potential decision outcomes (e.g. if a novel prey is red then, based on experience, it may be more likely to be identified as aposematic prey that should be avoided). Sampling social information can transform this prior expectation into a 'posterior probability' distribution (i.e. using Bayes' theorem). If the cost of acquiring information outweighs the utility of relying on prior knowledge, then the optimal action of the predator will shift (e.g. if a predator observes others consuming red palatable prey, this can provide social information that a novel red prey is undefended and the optimal action is to attack it). Experiments and modelling can be used to parameterise these values and determine potential evolutionary consequences for prey.

information to assess food patch quality seems to vary among species: European starlings *Sturnus vulgaris* (Templeton and Giraldeau 1995) and nine-spined sticklebacks *Pungitius pungitius* (Coolen et al. 2003) use social information about the profitability of food patches, but there is no evidence for this in Parid tits (Hillemann et al. 2020) or three-spined sticklebacks *Gasterosteus aculeatus* (Coolen et al. 2003). Social information use by predators for food searching may even drive formation of social structure: Ward and Zahavi's (1973) 'information centre hypothesis' proposes that communal roosts and breeding colonies evolved to serve as information centres about the location of food. However, local enhancement, where individuals are attracted to a site by the presence or cues of others (Thorpe 1956), has often provided a simpler explanation for how animals gain information about food sites (Mock et al. 1988, Richner and Heeb 1995).

An important first step in understanding how social effects can influence encounter rates is to determine which predator species in a community are more likely to use social information than others, and whether they use it to locate prey patches and/or assess patch quality. Predictions can be made based on the stochasticity or degree of patchiness of prey (Rafacz and Templeton 2003) as social information is expected to be of greater benefit when resources are unpredictable (Boyd and Richerson 1985). For example, social information about the location of schooling fish that are aggregated in constantly moving patches might be of great importance for foraging seabirds (Thiebault et al. 2014, Boyd et al. 2016). However, individuals within the same species also often vary in their tendency to use social information (Mesoudi et al. 2016), with some individuals preferring to search for food independently and some scrounging for food from others. Models of these two strategies treat them as frequency-dependent and predict them to occur at equilibrium when their payoffs are equal (Barnard and Sibly 1981). Food patch richness and encounter rate, as well as predator density, are predicted to influence the payoffs of each strategy (Beauchamp 2008) and competition can in theory constrain an individual's ability to use social information (Lee et al. 2016). Although intuitively appealing, these predictions have been rarely tested in the wild. Nevertheless, captive experiments have provided evidence of foragers converging on the predicted producer–scrounger equilibria (Mottley and Giraldeau 2000), and demonstrated that the tendency to use either strategy often depends on inherent individual characteristics, such as personality (Kurvers et al. 2010), dominance (Liker and Barta 2002) and learning ability (Katsnelson et al. 2011), or is influenced by current state (e.g. energy reserves, Lendvai et al. 2004) or ecological conditions (e.g. predation risk, Mathot and Giraldeau 2008). Variation in population structure and environmental conditions therefore adds a level of complexity to social transmission among predators that will need to be accounted for.

Predator population dynamics and age structure could also influence how social information use affects prey encounter rates. For example, inexperienced juveniles can acquire social information from their parents ('vertical transmission') either by responding to parents' active recruitment to good feeding sites (e.g. adult pied babblers *Turdoides bicolor* call inexperienced fledglings to food sources, Radford and Ridley 2006) or, more often, by following and observing their parents' foraging behaviour. This provides opportunities

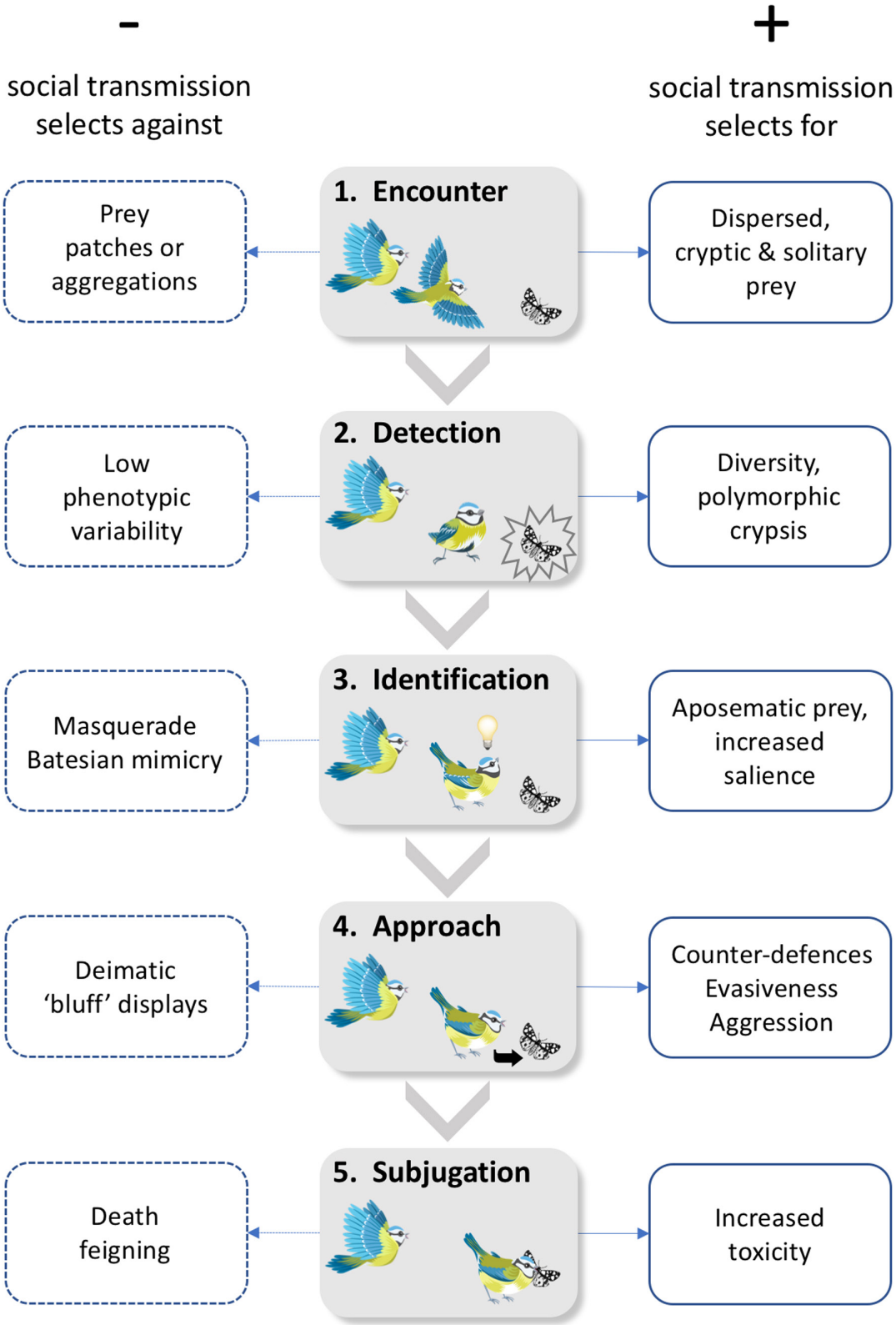

Figure 2. The predicted direction of selection on prey defences at each stage of the predation sequence when predators use social information. The predation stages include (Endler 1991): 1) encounter (getting within spatial and temporal proximity of prey), 2) detection (detecting prey against its background), 3) identification (identifying prey as edible), 4) approach (attacking and capturing the prey) and 5) subjugation and consumption (prey handling and ingestion). Credit for blue tit graphic: milovelen, Adobe Stock. Credit for tiger moth graphic: geraria, Adobe Stock.

to learn about profitable food sites and may shape foraging behaviour as adults: cross-fostering blue tit *Cyanistes caeruleus* and great tit *Parus major* nestlings shifted adult feeding niches in the direction of the foster species (Slagsvold and Wiebe 2007). However, socially acquired preferences may also be modified later in life. For example, after Franks et al. (2020a) experimentally seeded preferences for access-routes at feeding stations in a population of wild hihi *Notiomystis cincta*, they found that fledglings copied their parents, but these preferences disappeared once fledglings became independent. Instead, juveniles updated their choice over time and conformed to the behaviour of their peers (Franks et al. 2020a). The value of information from parents for young predators is likely to be sub-optimal in environments where prey abundance and distributions change over time, but whether updating of behaviour due to changes in social information occurs more often in stochastic environments is yet to be tested.

Given that social effects can influence encounter rates, social transmission among predators clearly needs to be incorporated into our understanding of predator population dynamics (Gil et al. 2018) and prey coevolution. For example, if predators are more likely to recruit others to food sites when prey are aggregated, and aggregations also provide more inadvertent cues about prey location, then social information use by predators could potentially alter selection and favour dispersed and solitary prey over prey aggregations (Fig. 2). However, while group living is expected to increase the risk of detection by predators and the cost of resource competition, it may also benefit prey by increasing antipredator vigilance and diluting individual risk of predation (Krause and Ruxton 2002). These tradeoffs vary among predator–prey systems, and further research is needed to understand how social transmission can change the relative costs and benefits of prey aggregation. In terms of producer–scrounger dynamics, we might expect prey to evolve crypsis (Fig. 2) or other characteristics that induce high rates of scrounging by predators, because this would lead to a smaller number of individuals searching for prey and lower foraging efficacy (Barrette and Giraldeau 2006, Hamblin et al. 2010). Support for this idea comes from experiments by Barrette and Giraldeau (2006) who found that nutmeg mannikins *Lonchura punctulata* increased scrounging when prey were cryptic and suggested that social predators could potentially favour crypsis. Similarly, Hamblin et al. (2010) predicted that prey should evolve more clumped distributions when predators are social because this is expected to increase scrounging and reduce individual search efficiency. However, their modelling approach showed that social transmission among predators actually selected for reduced clumping of prey, which was likely to be explained by non-linear effects of clump size on scrounging frequency (Hamblin et al. 2010). Apart from these studies, there are few other examples where social information transfer about prey location has been integrated into either verbal or explicit models of predator–prey coevolution, and this is a critical area for development.

2. Detection

After finding a potential foraging site, predators must detect the prey against its background. Previous work on crypsis has mainly focused on predator vision, visual conditions and viewing background (Ruxton et al. 2018), but not on how predators can influence each other's detection behaviour. In theory, observing others finding prey could encourage predators to pay more attention to their environment and therefore increase the likelihood that they also detect prey. It might also provide information on how to 'look for things' or increase a predator's persistence to search by providing positive information about the presence of prey (local enhancement, Thorpe 1956). Heterospecific information could be particularly important in this context as predator species differ in their visual abilities and their likelihood to detect prey (Endler 1978). This variation could be modelled with a producer–scrounger game (Barnard and Sibly 1981), where the difficulty of detecting prey could increase the number of scroungers that do not search for prey themselves (Barrette and Giraldeau 2006).

Experimental evidence of social information improving prey detection is, however, scarce. White and Gowan (2014) found that naïve brook trout *Salvelinus fontinalis* consumed more novel prey in the presence of a trained demonstrator and suggested that trout used social information to develop search images. In contrast, nutmeg mannikins did not increase consumption of cryptic food in the presence of an experienced conspecific; instead, interference from a naïve or an experienced conspecific actually reduced foraging efficiency (Courant and Giraldeau 2008). Competition from conspecifics may also influence a predator's decision to search for different prey types. In domestic chicks *Gallus gallus domesticus* more adventurous consumers decreased the consumption of familiar cryptic prey in the presence of a conspecific, and increased the acceptance of novel conspicuous prey that were easier to find (McMahon et al. 2014). However, this switch between familiar cryptic prey and novel conspicuous prey was not observed in chicks with higher dietary conservatism (McMahon et al. 2014). This demonstrates that the presence of other individuals can have complex effects on a predator's foraging behaviour, but how these different social effects influence a predator's search behaviour and prey detection is still poorly understood.

If social transmission improves the likelihood of predators to detect prey, this should influence selection pressures on prey defences (Turner 1964). However, mathematical models on frequency-dependent selection on prey types have traditionally considered only predators' personal search behaviour (Greenwood 1984), and we do not know how the strength of selection would change if social transmission of prey detection was included. For example, social acquisition of search images could favour rare prey phenotypes, which might speed up selection for diversity and polymorphism in cryptic prey (Fig. 2). Social transmission among predators could also influence the efficiency of other defences. Some prey confuse predators by performing unpredicted movements

(Scott-Samuel et al. 2015), and social information could provide a counter strategy for predators to quickly break this illusion if predators could learn about prey movements by observing the predation attempt of others. At the present, however, these ideas rely on conjecture and need to be tested experimentally.

3. Identification as profitable

In addition to detecting prey, predators need to assess the benefits of gaining nutrients against the potential costs of consuming prey to make adaptive foraging decisions (Sherratt 2003, Skelhorn et al. 2016, Marples et al. 2018). Promoting misidentification of these benefits and costs can be an effective defence. For example, masquerading prey avoid predation by resembling inedible objects, such as sticks, leaves and bird droppings (Skelhorn et al. 2010). The efficacy of masquerade depends on a predator's previous personal experience (Skelhorn et al. 2010) but predators might also be more likely to identify masquerading prey after witnessing others' attacks. This could make masquerade a less efficient strategy in communities where predators are social, but to our knowledge this has not been tested. By contrast, aposematic prey advertise their unprofitability (e.g. toxicity) with conspicuous warning signals (Poulton 1890), but to be an effective defence, predators must recognise the signal (Alatalo and Mappes 1996). Aposematic prey are therefore expected to suffer high predation from naïve predators, which makes the evolution and maintenance of aposematism paradoxical (Fisher 1930, Guilford 1988, Alatalo and Mappes 1996, Mappes et al. 2014). Social learning about prey defences provides one answer to this evolutionary puzzle because predators require fewer personal encounters with prey to adopt accurate identification (Guilford 1988, Thorogood et al. 2018). Accurate identification by predators also determines the success of mimetic defences. In Batesian mimicry, a palatable mimic resembles a defended model species and therefore gains protection from educated predators (Bates 1862). This creates a conflict between the model and the mimic as predators are predicted to increase their attacks on defended models when harmless mimics are abundant (Lindström et al. 1997). Similarly, palatable individuals ('automimics') in the population of an aposematic species can reduce predator avoidance learning (Brower et al. 1967). If social information use shapes predators' identification of prey, it could potentially impact a broad suite of prey defences. What evidence do we have that predators use social information to identify prey as profitable? Note that many of the examples we discuss below measure post-detection outcomes to attack or reject prey, but these depend on identification.

The first experimental studies to investigate if animals learn to avoid objects after observing aversive behavioural stimuli were by Klopfer with Muscovy ducks *Cairina moschata* and greenfinches *Chloris chloris*, but the number of tested individuals was too small to make strong conclusions about social information use (Klopfer 1957, 1959). Clearer evidence of 'social avoidance learning' came later from experiments with red-winged blackbirds *Agelaius phoeniceus* and common grackles *Quiscalus quiscula*, where birds avoided consuming food from a coloured cup after observing a demonstrator's negative foraging experience (Mason and Reidinger 1982, Mason et al. 1984). Similarly, in domestic chicks a disgust response of a conspecific (beak wiping and head shaking) influenced the observer's foraging choices (Johnston et al. 1998, Skelhorn 2011). However, there was no evidence of this when tested in hens (Sherwin et al. 2002), suggesting that social avoidance learning might be age-related. More recent studies have focused specifically on chemically defended prey, demonstrating that social transmission among predators reduces predation on novel aposematic prey under both captive conditions (Skelhorn 2011, Landová et al. 2017, Thorogood et al. 2018) and in the wild (Hämäläinen et al. 2021). Juvenile great tits learn to avoid aposematic firebugs faster after observing an educated conspecific refusing to attack them (Landová et al. 2017), and blue tits and great tits consume fewer novel aposematic prey after observing a negative foraging experience of a naïve conspecific (Thorogood et al. 2018, Hämäläinen et al. 2019) or a heterospecific (Hämäläinen et al. 2020, 2021). While most research has focused on avian predators, there is also evidence that vervet monkeys *Chlorocebus pygerythrus* (van de Waal et al. 2013) and cotton-top tamarins *Saguinus oedipus* (Snowdon and Boe 2003) can acquire avoidance to unpalatable food by observing the negative experience of others.

Observing foraging on palatable prey can also provide information that enhances predators' identification of prey. While there is evidence that Norway rats *Rattus norvegicus* can acquire a socially transmitted taste aversion under some conditions (Kuan and Colwill 1997), most studies find they do not learn socially to identify food as unpalatable (Galef et al. 1983, 1990, Galef and Whiskin 2000). Instead, rats use social information gathered from odour cues detected on the breath of others to identify palatable foods (Galef et al. 1983, 1990, Galef 1993). Many examples also exist from bird species, with red-winged blackbirds (Mason and Reidinger 1981), sparrows *Passer domesticus* (Fryday and Greig-Smith 1994) and domestic hens (Sherwin et al. 2002) preferring the same novel coloured food that they have observed conspecifics feeding on, or with many species preferring to feed from the same coloured food dish as the demonstrator (Mason et al. 1984, McQuoid and Galef 1993, Marchetti and Drent 2000, Benskin et al. 2002). Social information about palatability can also override previous experience of unpalatability. For example, fringe-lipped bats *Trachops cirrhosus* rapidly acquire a novel association between the call of a poisonous toad species and palatable prey after observing a positive foraging experience of a conspecific (Page and Ryan 2006). This type of reversal learning is particularly important when thinking about the identification, and fitness, of edible mimics (Turner 1964, Alcock 1969). In an early experiment, Alcock investigated fork-tailed flycatchers' *Tyrannus savana* attack rates on distasteful *Heliconius erato* butterflies and their edible mimics,

Anartia amathea, and found that birds were more likely to handle mimics after observing a conspecific consuming them (Alcock 1969). This suggests that social information about mimics can decrease their protection by shifting identification. However, more recent studies with artificial prey have provided mixed evidence of social information overriding personal experience with defended prey (Hämäläinen et al. 2019, 2021).

Taken together, we now have good evidence that social information about prey defences can reduce attacks on novel aposematic prey, and therefore facilitate the evolution of aposematism (Landová et al. 2017, Thorogood et al. 2018, Hämäläinen et al. 2019, 2020; Fig. 2). Because social transmission of avoidance is assumed to be beneficial for defended prey, we could also expect selection to favour prey traits that maximize opportunities for social learning about identification, such as increased distastefulness to elicit strong disgust responses (Brooke 2019), or more salient, multimodal warning signals (Rowe and Halpin 2013). However, understanding how prey can manipulate a predator's response to enhance social information use is unexplored. Social transmission also has potential to select against masquerade, automimicry and Batesian mimicry by providing predators with information about the presence of 'cheats' (Alcock 1969, Hämäläinen et al. 2021; Fig. 2), or facilitate generalisation of prey profitability to similar-looking prey. This could have implications for Müllerian mimicry where unprofitable species share a warning signal to reduce the cost of predator learning (Müller 1879), but how predators generalise socially acquired avoidance remains untested. More generally, if predators acquire enhanced identification of prey profitability through social transmission, this should influence how frequency-dependent selection operates. First, it may reduce selection for polymorphic prey by increasing identification of rarer morphs: predators are often hesitant to attack novel prey (Marples et al. 1998, Thomas et al. 2003), but social information from experienced or more adventurous individuals (Thornton 2008, McMahon et al. 2014), or simply the presence of another individual (Lalot et al. 2017), can decrease wariness and help predators to broaden their diet. Second, it may reduce protection for profitable mimics by reversing incorrect identification (Turner 1964, Alcock 1969, Mappes and Lindström 2012, Thorogood and Davies 2012, Hämäläinen et al. 2021). Nevertheless, there are differences among studies in how predators respond to social information about palatable and unpalatable prey, and understanding when, why and how predators combine social information to adjust their foraging requires investigation. Finding the answer to these questions is likely to depend on determining the costs and benefits of misidentification (Lynn 2005, Hämäläinen and Thorogood 2020) in relation to predator state (Sherratt 2003, Skelhorn et al. 2016) as well as determining the abundance of mimics and alternative prey, or different levels of competition among predators, which could all influence a predator's willingness to sample prey once they have been identified.

4. Approach

Once predators have identified prey as profitable and made a decision to attack, the next stage is to approach and capture prey. Social information can play an important role in improving the attack success if predators learn socially about hunting techniques (Krützen et al. 2005, Kitowski 2009, Brumm and Teschke 2012, Allen et al. 2013). In addition, prey have evolved many antipredator defences to avoid capture (Ruxton et al. 2018), and social information from other predators could help to overcome these. One example is deimatic displays where prey under attack suddenly undergo a transition, such as a change from cryptic to aposematic colouration, to frighten their predators (Umbers et al. 2015). This is an efficient strategy to stop the attack of naïve predators, but experienced individuals can learn to ignore the display (Umbers et al. 2019), and social transmission could facilitate this learning if predators observe others not responding to the display. However, it is also possible that observing a naïve individual being startled might instead reduce a predator's likelihood to approach the same prey, and these predictions need to be experimentally tested. In addition, predators might gain social information about the difficulty of capturing prey. Predators are predicted to avoid attacking evasive prey because of time and energy costs of unsuccessful attacks (Hasson 1991), and witnessing others failing to capture a prey could make predators less likely to approach it. Prey can also fight back when attacked (Mukherjee and Heithaus 2013), and an observation of others getting injured could warn predators about these defences, similar to social transmission of prey unprofitability (Mason and Reidinger 1982, Johnston et al. 1998, Thorogood et al. 2018). Social information about capture success might indeed influence a predator's initial decision to attack the prey (identification stage), rather than affecting their behaviour during capture, however, this has not received much experimental work.

Social transmission of hunting skills, on the other hand, is documented in several species, including extensive work in humans (Garfield et al. 2016). In non-human animals, a study with humpback whales *Megaptera novaeangliae* showed that social transmission had a major role in the spread of an innovative feeding technique, 'lobtail feeding' (Allen et al. 2013). Similar to other stages of a predation sequence, social information is expected to be particularly important for inexperienced juveniles that could improve their foraging success by observing predation events of adults. This was demonstrated in juvenile brown pelicans *Pelecanus occidentalis* that improved their foraging efficiency by following the plunge diving movements of adult birds (Brumm and Teschke 2012), and in marsh harriers *Circus aeruginosus* that performed more successful dives on prey when they were hunting with adults (Kitowski 2009). In some cases, predators have been suggested to learn tool-use behaviours by observing others (Krützen et al. 2005, Kenward et al. 2006, Schöning et al. 2008). This includes a bottlenose dolphin population (*Tursiops* sp.) where two foraging innovations, 'sponging' (carrying sponges on the rostra to probe into the

substrate for fish; Krützen et al. 2005), and 'shelling' (feeding on prey trapped inside conch shells; Wild et al. 2020) were found to spread socially among individuals. While both behaviours might improve prey capture, 'sponging' could also help dolphins to find the prey, and therefore influence prey detection stage. Tool-use in hunting has also been demonstrated in chimpanzees *Pan troglodytes* (Sanz et al. 2010) and New Caledonian crows *Corvus moneduloides* (Hunt 1996) that use stick tools to forage on invertebrates. However, these behaviours might be acquired through individual problem-solving and the role of social transmission remains unclear (Kenward et al. 2006, Schöning et al. 2008).

Social transmission of hunting skills can improve the foraging efficiency of predators (Kitowski 2009, Brumm and Teschke 2012), but its potential implications for prey are poorly understood. For example, the spread of novel foraging techniques among predators could be predicted to create new selection pressures for prey counter-defences (Fig. 2), and this is an underexplored mechanism for the evolution of multimodal defences. Selection could also favour evasiveness and defensive behaviours, such as aggression, if information about these defences spread socially among predators (Fig. 2). Alternatively, some prey benefit from mimicking a prey that is difficult to capture ('evasive Batesian mimicry'; Ruxton et al. 2004, Páez et al. 2021), and social transmission could alter these frequency-dependent model-mimic dynamics by providing predators with information about the presence of mimics. Similarly, social information could help predators to overcome other bluffing behaviours, such as deimatic displays in non-defended prey species (Fig. 2). There is therefore the intriguing potential of an arms race between predator and prey. However, failed predation attempts might happen very quickly and be difficult to observe, and it is possible that the opportunities to gather social information about capture success are fewer than at other stages of the predation sequence. Further work is therefore needed to understand how social information gathered from the attacks of others influences predators' attack decisions (identification stage) and capture success (approach stage).

5. Subjugation and consumption

The last two stages of a predation event are subjugation (preventing prey escape) and consumption (ingesting prey). Although they are traditionally considered as separate predation stages (Endler 1991), both of these happen after physical contact between the predator and the prey, and we have therefore combined them here. Predators must learn how to handle captured prey that vary in their ability to fight back and escape, and can also have mechanical defences, such as hairs, spines and stings (Mukherjee and Heithaus 2013, Ruxton et al. 2018). Observing others handling prey could influence a predator's decision to attack, but also provide social information on how to overcome these defences. For example, some avian predators have learned to remove stings (Davies 1977) or the most toxic parts of prey (Calvert et al. 1979, Fink and Brower 1981, Beckmann and Shine 2011) before consumption, and social transmission could facilitate this learning. These predators include black-backed orioles *Icterus abeillei* and black-headed grosbeaks *Pheucticus melanocephalus* that feed on toxic monarch butterflies *Danaus plexippus* by removing the body parts with the highest cardenolide content (Calvert et al. 1979, Fink and Brower 1981). Brower and Calvert (1985) suggested that the birds may learn and maintain this feeding behaviour via cultural transfer from one generation to the next, but this remains untested. So far, the only evidence of social transmission of prey-handling skills comes from meerkats *Suricata suricatta* that teach their pups to handle scorpions by gradually providing them dead, disabled (stings removed) or intact prey (Thornton and McAuliffe 2006). However, many species have been shown to use social information to solve novel artificial foraging problems (Palameta and Lefebvre 1985, Boogert et al. 2014, Gunhold et al. 2014, Aplin et al. 2015). This indicates that there is potential for similar learning about how to handle prey even though this has not been tested directly.

How social transmission during subjugation and consumption influences selection for prey defences has also received little attention. If predators could overcome prey defences by observing others removing mechanical defences or the most toxic parts of prey, this could potentially accelerate selection for stronger defences, such as increased toxicity (Fig. 2). Another antipredator defence to avoid consumption, and described in a wide range of taxa (Humphreys and Ruxton 2018), is death feigning. Social information could help predators to overcome this bluffing behaviour (Fig. 2), but this is yet to be investigated. Social transmission also has the potential to influence a predator's behaviour after consumption. Geophagy, the ingestion of clay soils, is observed in several bird (Downs et al. 2019) and mammal species (Krishnamani and Mahaney 2000), and is suggested to protect animals from toxic compounds in the diet due to its high capacity to absorb toxins (Krishnamani and Mahaney 2000, Downs et al. 2019). This behaviour could be transmitted socially in predator populations, but to our knowledge this has also not yet been investigated.

Conclusions

Throughout this review, we have discussed social information use by predators and drawn on existing empirical examples to explore whether this may shape the ecology and evolution of prey defences (Fig. 2). Many of our conclusions are tentative as studies testing the potential consequences of social transmission explicitly on predator–prey evolution are few. Furthermore, of the studies investigating social information use by predators specifically in the context of prey defence evolution, most have used only a few 'model predators' encountering simple prey communities with one palatable and unpalatable prey type (Johnston 1998, Skelhorn 2011, Landová et al. 2017, Thorogood et al. 2018, Hämäläinen et al. 2020). Heterogeneity among predators is

an important factor influencing the evolution of warning signals (Endler and Mappes 2004, Valkonen et al. 2012), and the complexity of the prey community influences the costs of predator learning and information use (Ihalainen et al. 2012). Similarly, most of this previous work has been conducted in captive conditions and with artificial prey, and only recently have studies started to investigate social transmission in wild predator populations (van de Waal et al. 2013, Aplin et al. 2015, Hämäläinen et al. 2021). Although captive work provides important insights into the mechanisms of social information use in controlled conditions, more field studies are needed to understand the efficacy of social transmission in complex environments with multiple information sources and varying costs and benefits. Nevertheless, the evidence gathered here suggests that testing predictions across the predation sequence would be a fruitful line of research (Box 1) and luckily, the expanding number of studies on animal social behaviour over recent decades mean that we have many well-established methods that can be adapted to investigate how social transmission can influence the ecological and evolutionary dynamics of predators and prey (Fig. 3).

More broadly, many questions still remain about information use and its effects on species coevolution and community dynamics that reach beyond predators and prey (Cantor et al. 2021). However, our review suggests that predator–prey interactions provide a useful paradigm. For example, we still understand little about among- and within-species variation in information use (Mesoudi et al. 2016) which is critical when considering interactions within ecological communities. Producer–scrounger dynamics could influence population demography and spatial distribution, for example, and also drive mixed species interactions in communities where heterospecific information is important (Gil et al. 2018). Mathematical models have also demonstrated that social information can induce positive density dependence on population growth rate, and result in information-mediated Allee effects (Schmidt et al. 2015). Schmidt et al. modelled information use in breeding habitat selection but similar models

Box 1. Future areas of research

Social information transfer can change species dynamics by modifying the behaviour or ecology of interacting species. However, models of coevolution or population and community dynamics have rarely considered how social transmission can change individuals' fitness. In the context of predator–prey interactions, social information use by predators could help to answer major ecological and evolutionary questions, such as the evolution and maintenance of prey defences, selection for prey distribution and composition of predator–prey communities. However, understanding whether and how social effects influence predator–prey dynamics requires 1) incorporating social transmission into models of predator–prey coevolution, 2) empirical studies in different predator–prey systems, preferably with both parties and 3) determining whether variability among individuals to use social information has adaptive significance (i.e. how different social learning strategies influence individuals' fitness). Social transmission among individuals also has the potential to shape how populations and communities respond to ongoing environmental change. There is therefore a pressing need to address these fundamental questions and consider how social transmission among predators and prey might affect practical decisions for conservation and resource management. Here we identify outstanding questions regarding social transmission among predators using the predation sequence framework; however, the stages are not independent of each other and some questions might fit in several categories.

1. Encounter
   - Do predators use social information about prey location more often in unpredictable environments?
   - How does social transmission among predators influence selection pressures for prey distribution?
2. Detection
   - Do predators use social information to develop search images?
   - Does social transmission among predators enhance selection for diversity in cryptic prey?
3. Identification
   - Can predators use social information to overcome masquerade?
   - How does the prey community's complexity influence predators' social information use?
   - How do predators generalise socially acquired avoidance/preference to similar-looking prey?
   - Do prey evolve traits that maximise social transmission of avoidance when predators are social (e.g. higher distastefulness)?
4. Approach
   - Can social information help predators overcome prey bluffing behaviours, such as deimatic displays in non-defended species?
   - Does social information about capture success influence a predator's decision to attack prey?
5. Subjugation and consumption
   - Do predators use social information to learn how to handle or ingest prey with mechanical defences or toxins?

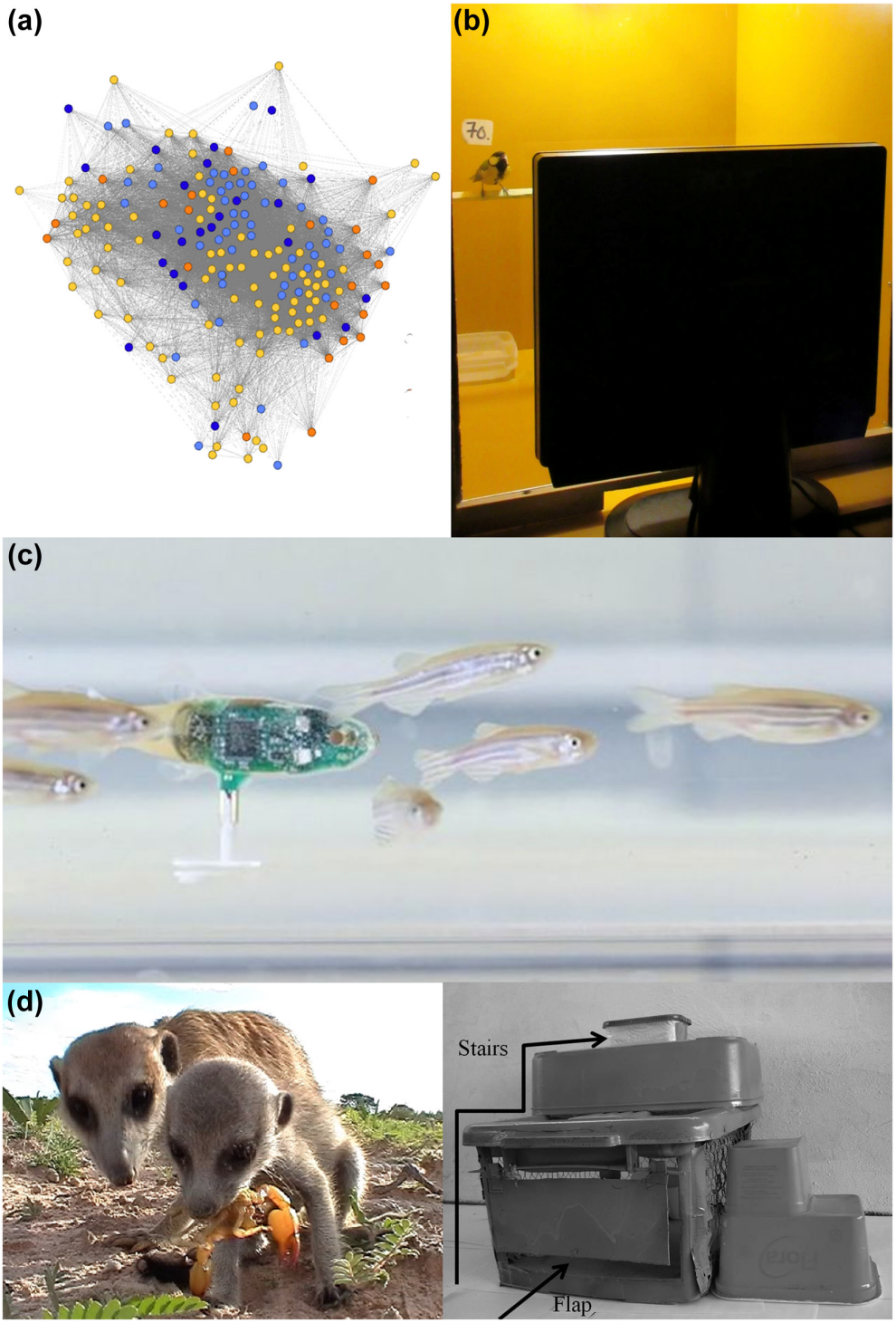

Figure 3. Examples of methods to study the role of social information use in predator–prey coevolution. (a) Social networks collected using radio-frequency identification tags on Parid tits can demonstrate social transmission of prey avoidance (Hämäläinen et al. 2021). Image by Liisa Hämäläinen. (b) Video playback to manipulate information provided by demonstrators can provide proof-of-concept for social learning (Thorogood et al. 2018). Image by Liisa Hämäläinen. (c) Robotics is an emerging method to manipulate demonstrator information (Bonnet et al. 2019). Image courtesy of Alain Herzog, EPFL. (d) Puzzle boxes can be used to study social learning of prey subjugation (Thornton and Malapert 2009). Images courtesy of Alex Thornton.

could be applied to a predator–prey context. For example, if predators rely strongly on social information to locate prey, this could result in Allee effects when the number of information producers in the predator community is low, which in turn could influence growth rates in prey populations. Social information use may also vary among populations depending on ecological conditions, such as food availability and predation pressure, but whether these differences are driven by evolutionary and/or developmental processes remains unknown (Chouinard-Thuly and Reader 2019). Nevertheless, heterogeneity among predators creates variable selection pressures for prey (Endler and Mappes 2004), and understanding variation in information use is therefore important if we are to explain complex predator–prey interactions. While we focused here on predators, social transmission among prey can similarly play an important role in predator–prey dynamics. Social information use by prey might, for example, influence predator detection (Ferrari et al. 2010, Magrath et al. 2015) or recognition (Brown 2003, Griffin 2004), and future work should therefore consider the information ecology of both parties.

Social transmission has the potential to modify how selection acts, and these genetic changes can in turn feedback on social transmission, but research on such gene-culture coevolution in many non-human animals, and particularly in predators, is only just beginning (Whitehead et al. 2019). One potential example comes from a recent study with killer whales *Orcinus orca* that found divergence between mammal-eating and fish-eating ecotypes in genes associated with digestion (Foote et al. 2016). This was suggested to result from cultural differentiation between the ecotypes, although demonstrating this causal association remains difficult (Foote et al. 2016). Similarly, we still understand little about how social transmission influences how selection is exerted on co-evolving species. A recent study incorporated social dynamics into modelling of evolution of host sociality and parasite virulence and found that it had striking implications for assumptions about host–parasite dynamics (Ashby and Farine 2021). Using a similar approach would provide insights into the effects of social transmission on coevolution between predators and prey at each stage of the predation sequence. Predictions from these models could then be tested with different predator–prey systems both in controlled laboratory experiments and with wild populations.

Finally, understanding social transmission among predators and prey has potential implications for conservation biology. For example, reintroduction is a common wildlife conservation strategy that rarely takes social structure and information transmission pathways into account (Brakes et al. 2019, Goldenberg et al. 2019, Franks et al. 2020b). However, social transmission could be harnessed to improve outcomes, both before and after release of the species to be conserved. For example, social information can provide a more efficient way to train individuals to recognise novel predators before their release (Brown and Laland 2001, Griffin 2004, Shier and Owings 2007, Rowell et al. 2020), or to train resident predators to avoid a novel prey species before it is introduced (Umbers et al. 2020). Maintaining or enhancing social transmission pathways during reintroductions may also reduce the time needed by reintroduced predators to recognise novel prey at the new site (Thorogood et al. 2018). Another successful technique is conditioned taste-aversion training that can be used to protect naïve local predators against toxic invasive potential prey species (Ward-Fear et al. 2016, Indigo et al. 2018), and understanding social transmission of avoidance could make these conservation efforts more effective. How animals use social information is also likely to change in future as many environments are changing rapidly because of human actions. For example, noise pollution can impair acoustic information, such as alarm calls (Grade and Sieving 2016, Templeton et al. 2016), and chemical pollutants can disrupt chemical information transfer about predators in aquatic systems (reviewed by van Donk et al. 2016). Understanding how social transmission shapes both evolutionary and ecological interactions among predators and prey is therefore both within our grasp, and becoming increasingly important if we are to predict how different species will respond to rapid and increasing human-induced changes in the environment.

Acknowledgements – We thank J. Szymkowiak and K. Schmidt for inviting us to contribute to this special issue.
Funding – LH was supported by Jenny and Antti Wihuri Foundation. HMR is supported by the Max Planck Society. JM was supported by the Academy of Finland (no. 320438) and the University of Jyväskylä. RT was supported by a start-up grant from the Helsinki Institute of Life Science (HiLIFE), University of Helsinki.
Conflict of interest – The authors have no conflict of interest to declare.

Author contributions

Liisa Hämäläinen: Conceptualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Hannah M. Rowland**: Conceptualization (equal); Writing – review and editing (equal). **Johanna Mappes**: Conceptualization (equal); Writing – review and editing (equal). **Rose Thorogood**: Conceptualization (equal); Writing – review and editing (equal).

Data availability statement

This article contain no original data.

References

Alatalo, R. V. and Mappes, J. 1996. Tracking the evolution of warning signals. – Nature 382: 708–710.
Alcock, J. 1969. Observational learning by fork-tailed flycatchers *Muscivora tyrannus*. – Anim. Behav. 17: 652–657.
Allen, J. et al. 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. – Science 340: 485–488.
Aplin, L. M. et al. 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. – Nature 518: 538–541.

Ashby, B. and Farine, D. R. 2021. Social information use shapes the coevolution of sociality and virulence. – Preprint at: <https://doi.org/10.1101/2020.10.02.323451>.
Barnard, C. J. and Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. – Anim. Behav. 29: 543–550.
Barrette, M. and Giraldeau, L. A. 2006. Prey crypticity reduces the proportion of group members searching for food. – Anim. Behav. 71: 1183–1189.
Bates, H. W. 1862. XXXII. Contributions to an insect Fauna of the Amazon Valley. Lepidoptera: Heliconidae. – Trans. Linn. Soc. Lond. 23: 495–566.
Beauchamp, G. 2008. A spatial model of producing and scrounging. – Anim. Behav. 76: 1935–1942.
Beckmann, C. and Shine, R. 2011. Toad's tongue for breakfast: exploitation of a novel prey type, the invasive cane toad, by scavenging raptors in tropical Australia. – Biol. Invas. 13: 1447–1455.
Benskin, C. M. H. et al. 2002. Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. – Anim. Behav. 64: 823–828.
Bonnet, F. et al. 2019. Robots mediating interactions between animals for interspecies collective behaviors. – Sci. Robot. 4: eaau7897.
Boogert, N. J. et al. 2014. Perching but not foraging networks predict the spread of novel foraging skills in starlings. – Behav. Processes 109: 135–144.
Boyd, C. et al. 2016. Effectiveness of social information used by seabirds searching for unpredictable and ephemeral prey. – Behav. Ecol. 27: 1223–1234.
Boyd, R. and Richerson, P. J. 1985. Culture and the evolutionary process. – Univ. of Chicago Press.
Brakes, P. et al. 2019. Animal cultures matter for conservation. – Science 363: 1032–1034.
Brooke, M. de L. 2019. Is eliciting disgust responses from its predators beneficial for toxic prey? – Anim. Behav. 155: 225–227.
Brower, L. P. and Calvert, W. H. 1985. Foraging dynamics of bird predators on overwintering monarch butterflies in Mexico. – Evolution 39: 852–868.
Brower, L. P. et al. 1967. Plant poisons in a terrestrial food chain. – Proc. Natl Acad. Sci. USA 57: 893–898.
Brown, C. and Laland, K. 2001. Social learning and life skills training for hatchery reared fish. – J. Fish Biol. 59: 471–493.
Brown, G. E. 2003. Learning about danger: chemical alarm cues and local risk assessment in prey fishes. – Fish Fish. 4: 227–234.
Brumm, H. and Teschke, I. 2012. Juvenile Galápagos pelicans increase their foraging success by copying adult behaviour. – PLoS One 7: e51881.
Calvert, W. H. et al. 1979. Mortality of the monarch butterfly (*Danaus plexippus* L.): avian predation at five overwintering sites in Mexico. – Science 204: 847–851.
Cantor, M. et al. 2021. The importance of individual-to-society feedbacks in animal ecology and evolution. – J. Anim. Ecol. 90: 27–44.
Chouinard-Thuly, L. and Reader, S. M. 2019. Population differences in how wild Trinidadian guppies use social information and socially learn. – Preprint at: <https://doi.org/10.1101/786772>.
Clark, R. W. 2007. Public information for solitary foragers: timber rattlesnakes use conspecific chemical cues to select ambush sites. – Behav. Ecol. 18: 487–490.
Coolen, I. et al. 2003. Species difference in adaptive use of public information in sticklebacks. – Proc. R. Soc. B 270: 2413–2419.
Courant, S. and Giraldeau, L. A. 2008. Conspecific presence makes exploiting cryptic prey more difficult in wild-caught nutmeg mannikins. – Anim. Behav. 75: 1101–1108.
Dall, S. R. X. et al. 2005. Information and its use by animals in evolutionary ecology. – Trends Ecol. Evol. 20: 187–193.
Danchin, E. et al. 2004. Public information: from nosy neighbors to cultural evolution. – Science 305: 487–491.
Davies, N. B. 1977. Prey selection and the search strategy of the spotted flycatcher *Muscicapa striata*: a field study on optimal foraging. – Anim. Behav. 25: 1016–1033.
Downs, C. T. et al. 2019. More than eating dirt: a review of avian geophagy. – Afr. Zool. 54: 1–19.
Elgar, M. A. 1986. House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. – Anim. Behav. 34: 169–174.
Emlen, J. T. 1952. Flocking behavior in birds. – Auk 69: 160–170.
Endler, J. A. 1978. A predator's view of animal color patterns. – Evol. Biol. 11: 319–364.
Endler, J. A. 1991. Interactions between predator and prey. – In: Krebs, J. R. and Davies, N. (eds), Behavioural ecology. Blackwell Scientific Publications, pp. 169–196.
Endler, J. A. and Mappes, J. 2004. Predator mixes and the conspicuousness of aposematic signals. – Am. Nat. 163: 532–547.
Farine, D. R. et al. 2015. Interspecific social networks promote information transmission in wild songbirds. – Proc. R. Soc. B 282: 20142804.
Ferrari, M. C. O. et al. 2010. Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. – Can. J. Zool. 88: 698–724.
Fink, L. S. and Brower, L. P. 1981. Birds can overcome the cardenolide defence of monarch butterflies in Mexico. – Nature 291: 67–70.
Fisher, R. A. 1930. The genetical theory of natural selection. – Clarendon Press.
Foote, A. D. et al. 2016. Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. – Nat. Commun. 7: 11693.
Franks, V. R. et al. 2020a. Foraging behaviour alters with social environment in a juvenile songbird. – Proc. R. Soc. B 287: 20201878.
Franks, V. R. et al. 2020b. Changes in social groups across reintroductions and effects on post-release survival. – Anim. Conserv. 23: 443–454.
Fryday, S. L. and Greig-Smith, P. W. 1994. The effects of social learning on the food choice of the house sparrow *Passer domesticus*. – Behaviour 128: 281–300.
Galef, B. G. 1993. Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission. – Anim. Behav. 46: 257–265.
Galef, B. G. and Whiskin, E. E. 2000. Demonstration of a socially transmitted flavor aversion in rats? Kuan and Colwill (1997) revisited. – Psychon. Bull. Rev. 7: 631–635.
Galef, B. G. et al. 1983. A failure to find socially mediated taste aversion learning in Norway rats *R. norvegicus*. – J. Comp. Psychol. 97: 358–363.
Galef, B. G. et al. 1990. Further evidence that Norway rats do not socially transmit learned aversions to toxic baits. – Anim. Learn. Behav. 18: 199–205.
Garfield, Z. H. et al. 2016. A cross-cultural analysis of hunter–gatherer social learning. – In: Terashima, H. and Hewlett, B. (eds), Social learning and innovation in contemporary hunter–gatherers. Springer, pp. 19–34.
Gil, M. A. et al. 2018. Social information links individual behavior to population and community dynamics. – Trends Ecol. Evol. 33: 535–548.

Gillam, E. H. 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. – Can. J. Zool. 85: 795–801.
Goldenberg, S. Z. et al. 2019. Increasing conservation translocation success by building social functionality in released populations. – Global Ecol. Conserv. 18: e00604.
Grade, A. M. and Sieving, K. E. 2016. When the birds go unheard: highway noise disrupts information transfer between bird species. – Biol. Lett. 12: 20160113.
Greenwood, J. J. D. 1984. The functional basis of frequency-dependent food selection. – Biol. J. Linn. Soc. 23: 177–199.
Griffin, A. S. 2004. Social learning about predators: a review and prospectus. – Anim. Learn. Behav. 32: 131–140.
Guilford, T. 1988. The evolution of conspicuous coloration. – Am. Nat. 131: S7–S21.
Gunhold, T. et al. 2014. Video demonstrations seed alternative problem-solving techniques in wild common marmosets. – Biol. Lett. 10: 20140439.
Hamblin, S. et al. 2010. Predator inadvertent social information use favours reduced clumping of its prey. – Oikos 119: 286–291.
Hasson, O. 1991. Pursuit-deterrent signals: communication between prey and predator. – Trends Ecol. Evol. 6: 325–329.
Hillemann, F. et al. 2019. Diurnal variation in the production of vocal information about food supports a model of social adjustment in wild songbirds. – Proc. R. Soc. B 286: 20182740.
Hillemann, F. et al. 2020. Information use in foraging flocks of songbirds: no evidence for social transmission of patch quality. – Anim. Behav. 165: 35–41.
Hughes, N. K. et al. 2012. Dangerous liaisons: the predation risks of receiving social signals. – Ecol. Lett. 15: 1326–1339.
Humphreys, R. K. and Ruxton, G. D. 2018. A review of thanatosis (death feigning) as an anti-predator behaviour. – Behav. Ecol. Sociobiol. 72: 22.
Hunt, G. R. 1996. Manufacture and use of hook-tools by New Caledonian crows. – Nature 379: 249–251.
Hämäläinen, L. and Thorogood, R. 2020. The signal detection problem of aposematic prey revisited: integrating prior social and personal experience. – Phil. Trans. R. Soc. B 375: 20190473.
Hämäläinen, L. et al. 2019. Social information use about novel aposematic prey is not influenced by a predator's previous experience with toxins. – Funct. Ecol. 33: 1982–1992.
Hämäläinen, L. et al. 2020. Social learning within and across predator species reduces attacks on novel aposematic prey. – J. Anim. Ecol. 89: 1153–1164.
Hämäläinen, L. et al. 2021. Social transmission in the wild can reduce predation pressure on novel aposematic prey signals. – Nat. Commun. 12: 3978.
Ihalainen, E. et al. 2012. Prey community structure affects how predators select for Müllerian mimicry. – Proc. R. Soc. B 279: 2099–2105.
Indigo, N. et al. 2018. Not such silly sausages: evidence suggests northern quolls exhibit aversion to toads after training with toad sausages. – Austral Ecol. 43: 592–601.
Iwasa, Y. et al. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. – Am. Nat. 117: 710–723.
Johnston, A. et al. 1998. Observation learning in day-old chicks using a one-trial passive avoidance learning paradigm. – Anim. Behav. 56: 1347–1353.
Judd, T. M. and Sherman, P. W. 1996. Naked mole-rats recruit colony mates to food sources. – Anim. Behav. 52: 957–969.
Katsnelson, E. et al. 2011. Individual-learning ability predicts social-foraging strategy in house sparrows. – Proc. R. Soc. B 278: 582–589.
Kawamori, A. and Matsushima, T. 2010. Subjective value of risky foods for individual domestic chicks: a hierarchical Bayesian model. – Anim. Cogn. 13: 431–441.
Kenward, B. et al. 2006. Development of tool use in New Caledonian crows: inherited action patterns and social influences. – Anim. Behav. 72: 1329–1343.
Kitowski, I. 2009. Social learning of hunting skills in juvenile marsh harriers *Circus aeruginosus*. – J. Ethol. 27: 327–332.
Klopfer, P. H. 1957. An experiment on empathic learning in ducks. – Am. Nat. 91: 61–63.
Klopfer, P. H. 1959. Social interactions in discrimination learning with special reference to feeding behavior in birds. – Behaviour 14: 282–299.
Krause, J. and Ruxton, G. D. 2002. Living in groups. – Oxford Univ. Press.
Krebs, J. R. 1973. Behavioral aspects of predation. – In: Bateson, P. P. G. and Klopfer, P. H. (eds), Perspectives in ethology. Plenum, pp. 73–111.
Krishnamani, R. and Mahaney, W. C. 2000. Geophagy among primates: adaptive significance and ecological consequences. – Anim. Behav. 59: 899–915.
Krützen, M. et al. 2005. Cultural transmission of tool use in bottlenose dolphins. – Proc. Natl Acad. Sci. USA 102: 8939–8943.
Kuan, L. A. and Colwill, R. M. 1997. Demonstration of a socially transmitted taste aversion in the rat. – Psychon. Bull. Rev. 4: 374–377.
Kurvers, R. H. J. M. et al. 2010. The effect of personality on social foraging: shy barnacle geese scrounge more. – Proc. R. Soc. B 277: 601–608.
Laland, K. N. and Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. – Anim. Behav. 53: 1161–1169.
Lalot, M. et al. 2017. You know what? I'm happy. Cognitive bias is not related to personality but is induced by pair-housing in canaries *Serinus canaria*. – Behav. Processes 134: 70–77.
Landová, E. et al. 2017. The effect of social learning on avoidance of aposematic prey in juvenile great tits *Parus major*. – Anim. Cogn. 20: 855–866.
Lee, A. E. G. et al. 2016. Information use and resource competition: an integrative framework. – Proc. R. Soc. B 283: 20152550.
Lendvai, Á. Z. et al. 2004. The effect of energy reserves on social foraging: hungry sparrows scrounge more. – Proc. R. Soc. B 271: 2467–2472.
Liker, A. and Barta, Z. 2002. The effects of dominance on social foraging tactic use in house sparrows. – Behaviour 139: 1061–1076.
Lindström, L. et al. 1997. Imperfect Batesian mimicry – the effects of the frequency and the distastefulness of the model. – Proc. R. Soc. B 264: 149–153.
Lynn, S. K. 2005. Learning to avoid aposematic prey. – Anim. Behav. 70: 1221–1226.
Magrath, R. D. et al. 2015. Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. – Biol. Rev. 90: 560–586.
Mappes, J. and Lindström, L. 2012. How did cuckoo get its polymorphic plumage? – Science 337: 532–533.
Mappes, J. et al. 2014. Seasonal changes in predator community switch the direction of selection for prey defences. – Nat. Commun. 5: 5016.
Marchetti, C. and Drent, P. J. 2000. Individual differences in the use of social information in foraging by captive great tits. – Anim. Behav. 60: 131–140.

Marples, N. M. et al. 1998. Responses of wild birds to novel prey: evidence of dietary conservatism. – Oikos 83: 161–165.
Marples, N. M. et al. 2018. An individual-based profitability spectrum for understanding interactions between predators and their prey. – Biol. J. Linn. Soc. 125: 1–13.
Mason, J. R. and Reidinger, R. F. 1981. Effects of social facilitation and observational learning on feeding behavior of the red-winged blackbird *Agelaius phoeniceus*. – Auk 98: 778–784.
Mason, J. R. and Reidinger, R. F. 1982. Observational learning of food aversions in red-winged blackbirds *Agelaius phoeniceus*. – Auk 99: 548–554.
Mason, J. R. et al. 1984. Comparative assessment of food preferences and aversions acquired by blackbirds via observational learning. – Auk 101: 796–803.
Mathot, K. J. and Giraldeau, L. A. 2008. Increasing vulnerability to predation increases preference for the scrounger foraging tactic. – Behav. Ecol. 19: 131–138.
McMahon, K. et al. 2014. Dietary wariness influences the response of foraging birds to competitors. – Anim. Behav. 89: 63–69.
McNamara, J. and Houston, A. 1980. The application of statistical decision theory to animal behaviour. – J. Theor. Biol. 85: 673–690.
McQuoid, L. M. and Galef, B. G. 1993. Social stimuli influencing feeding behaviour of Burmese fowl: video analysis. – Anim. Behav. 46: 13–22.
Mesoudi, A. et al. 2016. The evolution of individual and cultural variation in social learning. – Trends Ecol. Evol. 31: 215–225.
Mock, D. W. et al. 1988. Falsifiability and the information centre hypothesis. – Ornis Scand. 19: 231–248.
Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. – Ecol. Monogr. 40: 119–168.
Mottley, K. and Giraldeau, L. A. 2000. Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria. – Anim. Behav. 60: 341–350.
Mukherjee, S. and Heithaus, M. R. 2013. Dangerous prey and daring predators: a review. – Biol. Rev. 88: 550–563.
Müller, F. 1879. Ituna and Thyridia: a remarkable case of mimicry in butterflies. – Trans. R. Entomol. Soc. Lond. 20–29.
Norbury, G. L. et al. 2021. Misinformation tactics protect rare birds from problem predators. – Sci. Adv. 7: eabe4164.
Olsson, O. and Brown, J. S. 2006. The foraging benefits of information and the penalty of ignorance. – Oikos 112: 260–273.
Olsson, O. and Holmgren, N. M. A. 1998. The survival-rate-maximizing policy for Bayesian foragers: wait for good news. – Behav. Ecol. 9: 345–353.
Páez, E. et al. 2021. Hard to catch: experimental evidence supports evasive mimicry. – Proc. R. Soc. B 288: 20203052.
Page, R. A. and Ryan, M. J. 2006. Social transmission of novel foraging behavior in bats: frog calls and their referents. – Curr. Biol. 16: 1201–1205.
Palameta, B. and Lefebvre, L. 1985. The social transmission of a food-finding technique in pigeons: what is learned? – Anim. Behav. 33: 892–896.
Penndorf, J. and Aplin, L. 2020. Environmental and life history factors, but not age, influence social learning about food: a meta-analysis. – Anim. Behav. 167: 161–176.
Poulton, E. B. 1890. The colours of animals, their meaning and use, especially considered in the case of insects. – Kegan Paul, Trench, Trübner & Co.
Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings *Sturnus vulgaris* in relation to predation and foraging. – Anim. Behav. 22: 501–505.
Pulliam, H. R. 1973. On the advantages of flocking. – J. Theor. Biol. 38: 419–422.
Pyke, G. H. et al. 1977. Optimal foraging: a selective review of theory and tests. – Q. Rev. Biol. 52: 137–154.
Radford, A. N. and Ridley, A. R. 2006. Recruitment calling: a novel form of extended parental care in an altricial species. – Curr. Biol. 16: 1700–1704.
Rafacz, M. and Templeton, J. J. 2003. Environmental unpredictability and the value of social information for foraging starlings. – Ethology 109: 951–960.
Richner, H. and Heeb, P. 1995. Is the information centre hypothesis a flop? – Adv. Study Behav. 24: 1–46.
Rowe, C. and Halpin, C. 2013. Why are warning displays multimodal? – Behav. Ecol. Sociobiol. 67: 1425–1439.
Rowell, T. A. et al. 2020. Predator-awareness training in terrestrial vertebrates: progress, problems and possibilities. – Biol. Conserv. 252: 108740.
Ruxton, G. D. et al. 2004. Evasive mimicry: when (if ever) could mimicry based on difficulty of capture evolve? – Proc. R. Soc. B 271: 2135–2142.
Ruxton, G. D. et al. 2018. Avoiding attack: the evolutionary ecology of crypsis, aposematism and mimicry, 2nd edn. – Oxford Univ. Press.
Sanz, C. M. et al. 2010. Chimpanzees prey on army ants with specialized tool set. – Am. J. Primatol. 72: 17–24.
Schmidt, K. A. et al. 2015. Information-mediated Allee effects in breeding habitat selection. – Am. Nat. 186: E162–E171.
Schöning, C. et al. 2008. The nature of culture: technological variation in chimpanzee predation on army ants revisited. – J. Hum. Evol. 55: 48–59.
Scott-Samuel, N. E. et al. 2015. Moving in groups: how density and unpredictable motion affect predation risk. – Behav. Ecol. Sociobiol. 69: 867–872.
Sheriff, M. J. et al. 2020. Proportional fitness loss and the timing of defensive investment: a cohesive framework across animals and plants. – Oecologia 193: 273–283.
Sherratt, T. N. 2003. State-dependent risk-taking by predators in systems with defended prey. – Oikos 103: 93–100.
Sherwin, C. M. et al. 2002. Social learning influences the preferences of domestic hens for novel food. – Anim. Behav. 63: 933–942.
Shier, D. M. and Owings, D. H. 2007. Effects of social learning on predator training and postrelease survival in juvenile black-tailed prairie dogs, *Cynomys ludovicianus*. – Anim. Behav. 73: 567–577.
Skelhorn, J. 2011. Colour biases are a question of conspecifics taste. – Anim. Behav. 81: 825–829.
Skelhorn, J. et al. 2010. Masquerade: camouflage without crypsis. – Science 327: 51.
Skelhorn, J. et al. 2016. Learning about aposematic prey. – Behav. Ecol. 27: 955–964.
Slagsvold, T. and Wiebe, K. L. 2007. Learning the ecological niche. – Proc. R. Soc. B 274: 19–23.
Snowdon, C. T. and Boe, C. Y. 2003. Social communication about unpalatable foods in tamarins *Saguinus oedipus*. – J. Comp. Psychol. 117: 142–148.
Templeton, C. N. et al. 2016. Traffic noise drowns out great tit alarm calls. – Curr. Biol. 26: R1173–R1174.
Templeton, J. J. and Giraldeau, L. A. 1995. Patch assessment in foraging flocks of European starlings: evidence for the use of public information. – Behav. Ecol. 6: 65–72.
Thiebault, A. et al. 2014. From colony to first patch: processes of prey searching and social information in Cape gannets. – Auk 131: 595–609.

Thomas, R. J. et al. 2003. Dietary conservatism may facilitate the initial evolution of aposematism. – Oikos 101: 458–466.
Thornton, A. 2008. Social learning about novel foods in young meerkats. – Anim. Behav. 76: 1411–1421.
Thornton, A. and Malapert, A. 2009. Experimental evidence for social transmission of food acquisition techniques in wild meerkats. – Anim. Behav. 78: 255–264.
Thornton, A. and McAuliffe, K. 2006. Teaching in wild meerkats. – Science 313: 227–229.
Thorogood, R. and Davies, N. B. 2012. Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. – Science 337: 578–580.
Thorogood, R. et al. 2018. Social transmission of avoidance among predators facilitates the spread of novel prey. – Nat. Ecol. Evol. 2: 254–261.
Thorpe, W. H. 1956. Learning and instinct in animals. – Harvard Univ. Press.
Turner, E. R. A. 1964. Social feeding in birds. – Behaviour 24: 1–45.
Umbers, K. D. L. et al. 2015. Deimatic displays. – Curr. Biol. 25: R58–R59.
Umbers, K. D. L. et al. 2019. The protective value of a defensive display varies with the experience of wild predators. – Sci. Rep. 9: 463.
Umbers, K. D. L. et al. 2020. Educating the enemy: harnessing learned avoidance behavior in wild predators to increase survival of reintroduced southern corroboree frogs. – Conserv. Sci. Pract. 2: e139.
Valkonen, J. K. et al. 2012. Variation in predator species abundance can cause variable selection pressure on warning signaling prey. – Ecol. Evol. 2: 1971–1976.
van de Waal, E. et al. 2013. Potent social learning and conformity shape a wild primate's foraging decisions. – Science 340: 483–485.
van Donk, E. et al. 2016. Pharmaceuticals may disrupt natural chemical information flows and species interactions in aquatic systems: ideas and perspectives on a hidden global change. – In: Gunther, F. A. and de Voogt, P. (eds), Reviews of environmental contamination and toxicology. Springer, pp. 91–105.
van Gils, J. A. et al. 2003. Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. – Am. Nat. 161: 777–793.
Ward, P. and Zahavi, A. 1973. The importance of certain assemblages of birds as 'information-centres' for food-finding. – Ibis 115: 517–534.
Ward-Fear, G. et al. 2016. Ecological immunization: in situ training of free-ranging predatory lizards reduces their vulnerability to invasive toxic prey. – Biol. Lett. 12: 20150863.
White, S. L. and Gowan, C. 2014. Social learning enhances search image acquisition in foraging brook trout. – Environ. Biol. Fishes 97: 523–528.
Whitehead, H. et al. 2019. The reach of gene-culture coevolution in animals. – Nat. Commun. 10: 2405.
Wild, S. et al. 2020. Integrating genetic, environmental and social networks to reveal transmission pathways of a dolphin foraging innovation. – Curr. Biol. 30: 3024–3030.