ORIGINAL ARTICLE

Joint evolution of traits for social learning

Cameron Rouse Turner[1] · Stephen Francis Mann[2,3] · Matt Spike[4] · Robert D. Magrath[5] · Kim Sterelny[6]

Abstract

Animals vary in the sophistication of their capacities for social learning, and much research has focused on establishing when learning from others is favourable. However, social learning involves both a receiver (who learns), and a sender (who is learned from). Surprisingly, the joint evolution of traits for social learning has attracted little attention, even though learning by the receiver has consequences for the fitness of the sender. Accordingly, animals are observed to teach and mask, and thereby influence available information. Here, we provide a mathematical model to examine when reliable social learning emerges as a result of investment in traits for social and asocial learning, as well as teaching and masking. Our purpose is to provide a general framework for thinking about how social learning is impacted by sender-receiver joint evolution, so our model is heuristic; its aim is to delineate broad categories of direct and indirect selection on learning traits. Our findings lead us to theorise that social learning exists on a continuum. At one extreme, senders and receivers have strongly opposed interests, selecting for masking to combat informational parasitism; at the other extreme, strongly aligned interests lead to teaching to enhance social learning. Sophisticated, metabolically expensive traits for influencing social learning can evolve under either aligned or opposed interests, although the aim of their design differs. Furthermore, we find that traits for asocial learning should often be more sophisticated than traits for receiving, while receiving traits should often be more sophisticated than sender traits for teaching or masking.

Significance statement

Learning from group members is often crucial for survival, with social learning influencing the development of behaviours in domains as diverse as foraging, mate preference, and predator defence. Formal modelling has provided a good understanding of the conditions that favour social learning, given animals already have the ability to learn asocially. However, the success of social learning also depends on the behaviour of the group member who is learned from. For instance, group members may teach others how to hunt dangerous prey. Alternatively, knowledgeable individuals sometimes take actions to hinder learning, for instance, by disguising the location of a food cache. Here, we provide a unitary mathematical framework to study how behaviours of the group member who is learned from jointly evolve with those of the learner.

✉ Cameron Rouse Turner
c.rouse.turner@princeton.edu

1   Computational Cognitive Science Lab, Department of Computer Science, Princeton University, Princeton 08540, USA

2   LOGOS Research Group, Faculty of Philosophy, Universitat de Barcelona, 08001 Barcelona, Spain

3   Department of Linguistic and Cultural Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Pl. 6, 04103 Leipzig, Germany

4   Centre for Language Evolution, School of Philosophy, Psychology and Language Sciences, The University of Edinburgh, Edinburgh EH8 9AD, UK

5   Division of Ecology & Evolution, Research School of Biology, Australian National University, Canberra 2601, Australia

6   School of Philosophy, Research School of Social Sciences, Australian National University, Canberra 2601, Australia

Introduction

In 1935, Hawaiian cane toads, *Bufo marinus*, were introduced to Australia, becoming a devastating invasive species as their skin toxins killed native fauna. The Torresian crow, *Corvus orru*, avoided this threat, by learning to flip the toad over to eat the non-poisonous underbelly, and this behaviour then spread rapidly through observation (Donato and Potts 2004). Social learning is present across diverse taxa, but animals vary in their capacities for learning from others (Heyes 1994; Shettleworth 2009; Hoppitt and Laland 2013; Stevens 2013; Aplin 2019; Whitehead and Rendell 2015). Consequently, animal cultures also vary in their sophistication (Mesoudi and Thornton 2018; Whiten 2019). As the Torresian crow demonstrates, social learning can have significant advantages, allowing behaviour to be rapidly tailored to changes in the environment, as well as reducing the costs of potentially lethal trial-and-error learning. Further, the highly sophisticated cumulative culture possessed by humans has been credited for our extraordinary success as a species (Boyd et al. 2011; Henrich 2015; Laland 2017). The apparent benefits gained by social learning present us with a puzzle: why do some species have sophisticated capacities that allow reliable social learning, but not others?

Social learning appears to be favoured when the behaviour being learned is beneficial, yet costly to acquire by asocial learning. Given that animals can learn asocially, much theoretical effort has focused on the conditions that favour social learning. A general result is that social learning is selected when learnable behaviours cannot be attained as cheaply by asocial learning, and others have already paid the costs of acquiring the behaviour asocially (Barnard and Sibly 1981; Boyd and Richerson 1985; Rogers 1988; Laland and Kendal 2003; Rendell et al. 2010; Afshar and Giraldeau 2014; Aoki and Feldman 2014; Laland 2017; Montrey and Shultz 2020). Conversely, social learning will be selected against if social information is likely to be out-of-date or less reliable than personal information.

In contrast to work that focuses on traits for receiving, there has been little attention on traits of the sender. The *sender* produces information, while the *receiver* gains the information and so learns the behaviour. It is not required that senders intentionally or consciously provide information, although they may. Animals may be in the role of receiver and sender at different times, or for different behaviours. In much previous formal theory, the only strategy available to senders (producers) is to switch roles to being a receiver (scrounger) (reviewed Laland and Kendal 2011; Afshar and Giraldeau 2014; Aoki and Feldman 2014; Chimento et al. 2022).

Research on senders' traits has mainly examined the evolution of *teaching*, defined as senders modifying their usual behavioural repertoire to actively facilitate social learning in others (Hoppitt et al. 2008; Thornton and Raihani 2008). Kin selection models show that teaching is favoured when the benefit of helping a relative learn is greater than the cost of the effort to teach, and when the behaviour cannot readily be acquired through asocial learning or inadvertent social information (Fogarty et al. 2011).

The overall lack of broad formal theory about the sender's traits is surprising, as social learning clearly produces selection on the sender as well as the receiver. In particular, whenever benefits are conferred socially as a consequence of behaviour, selection will act both on actor and recipient (Hamilton 1964; Lehmann and Keller 2006; West et al. 2007). Benefits arise from social learning, in the form of information about how to perform adaptive behaviours; therefore, social learning should also lead to selection on the sender (Sterelny 2003; Danchin et al. 2004; Dall et al. 2005). Signalling theory has considered the conditions under which overlapping interests of sender and receiver allow a communication system to be stable (Maynard Smith and Harper 2003; Searcy and Nowicki 2005; Bradbury and Vehrencamp 2011), but formal models have generally not studied how communication emerges from the use of inadvertent cues (exceptions include Skyrms 2010; Scott-Phillips et al. 2012; Wiley 2013; Hackett et al. 2016; Miller et al. 2020). This is despite the fact that the hypothesis that communication evolves through ritualisation has a long history (reviewed Bradbury and Vehrencamp 2011; Scott et al. 2010). Signalling models also generally consider when a communicatory signal is used to respond to an immediate environmental contingency, and are not framed as studying the learning of new behaviours. Further, signalling models do not cover the evolution of all social information use capacities, because they do not include the alternative strategy of asocial learning.

While teaching may arise when the sender gains sufficient benefits, senders may also evolve to hinder social learning when they face sufficient costs (Byrne and Whiten 1985; Whiten and Byrne 1988; Hare et al. 2001; Held et al. 2002, 2010; Clayton et al. 2007; Grodzinski and Clayton 2010; Stevens 2013). Senders who perform a novel advantageous behaviour have a fitness advantage over naive competitors. That advantage is reduced when a conspecific learns, and this provides an evolutionary motivation to hinder learning by masking. For instance, baboons (*Papio ursinus*) wait until others have left the area before going to the location of food (Byrne and Whiten 1985).

The fitness effects of sending may not always be sufficient to produce adaptations that facilitate or hinder social learning. Senders may leak sufficient inadvertent information to allow learning through their routine activities, and these activities may also be too costly to disrupt in order to enhance or reduce information (Fogarty et al. 2011).

Nevertheless, instances of teaching and masking do occur in nature, and appear to greatly influence the reliability of social learning (Byrne and Whiten 1985; Whiten and Byrne 1988; Clayton et al. 2007; Hoppitt et al. 2008; Thornton and Raihani 2008; Clarke 2010; Held et al. 2010).

Here, we provide a mathematical framework that examines the joint evolution of traits affecting learning, and establishes broad conditions under which there is selection to promote highly reliable social learning. Social evolutionary theory implies that social learning should lead to selection on the traits of both the sender and receiver (Hamilton 1964; Lehmann and Keller 2006; West et al. 2007), with previous work on teaching and masking supporting this idea (Whiten and Byrne 1988; Hoppitt et al. 2008; Thornton and Raihani 2008; Fogarty et al. 2011; Stevens 2013). Further, previous work suggests that the evolution of traits for asocial learning should also affect social learning (Boyd and Richerson 1985; Rogers 1988; Laland and Kendal 2003; Rendell et al. 2010; Afshar and Giraldeau 2014; Aoki and Feldman 2014; Montrey and Shultz 2020). However, it is unclear how this related work fits together, and whether a unitary model can uncover general principles about the joint evolution of traits involved with learning. We provide a heuristic model that delineates important categories of direct and indirect selection on traits involved with learning (Hamilton 1964). Our aim is to give broad indications about how traits influencing learning jointly evolve, so we give a simplistic treatment of issues such as frequency and density dependence, culture, and kin selection. Animals may invest in traits for social learning (receiving) and asocial learning, as well as in traits for teaching (aiding learning), or masking (hindering learning). However, as phenotypic investment in learning is a drain on resources, these adaptations are costly to build and maintain. Next, we explain the key concepts used in the model, and then outline the formalism.

Traits that affect learning

Whether a behaviour is successfully acquired is dictated by how well an animal can use information indicating which actions to perform and in what context (Heyes 1994; Coussi-Korbel and Fragaszy 1995; Sterelny 2003; Danchin et al. 2004; Dall et al. 2005). Our model describes the joint evolution of *learning traits* that change the success or *reliability* of learning by improving or degrading usable information. That is, we consider how traits involved in sending, receiving, and asocial learning are impacted when learning occurs, as well as affect each other's evolution.

Animals vary in traits for using personally acquired information to learn asocially, and for receiving information from others to learn socially (Heyes 1994; Shettleworth 2009; Hoppitt and Laland 2013; Stevens 2013; Aplin 2019; Whiten 2019; Whitehead and Rendell 2015). Traits that allow more

reliable asocial learning include those for registering changing aspects of the environment, or rapidly assimilating new information. Analogous traits that lead to reliable social learning include paying close attention to others, or to the products of their behaviour, and being able to imitate or learn quickly from what is observed. For example, when presented with novel tasks, the highly social pinyon jay (*Gymnorhinus cyanocephalus*) has greater success using social information than personal information alone; whereas, the closely related Clark's nutcracker (*Nucifraga columbiana*), a less social species, does not have greater success by leveraging social information (Templeton et al. 1999). Similarly, while nine-spine sticklebacks (*Pungitius pungitius*) can learn about food patches by using social information from the location of others, the closely related three-spined stickleback (*Gasterosteus aculeatus*) cannot use social information in this way (Laland et al. 2011). This is despite the fact that the two species perform similarly on asocial learning tasks. This difference in social learning is likely because nine-spines are preferred by predators due to their weaker amour, which favours learning by observation from cover.

Sending traits influence the production of information leading to receiver learning, and so can be further divided into teaching traits or masking traits. Although we focus on behavioural sending traits, sending traits could also be morphological, such as brightly coloured plumage that signals mate quality. There is substantial variation in the *teaching* traits of animals that make more social information available. Teaching can include greater tolerance of observers, providing appropriate demonstrations, or deliberate communication (Hoppitt et al. 2008; Thornton and Raihani 2008, 2010; Hoppitt and Laland 2013). We employ a permissive definition of teaching as any form of cooperative behaviour that functions to facilitate learning in others (Thornton and Raihani 2008). For example, the white-tailed ptarmigan (*Lagopus leucurus*) teaches its chicks about nutritional content by producing calls and tid-bitting displays in the presence of high protein food (Clarke 2010). Here, the propensity to produce the tid-bitting display to draw attention to food is the teaching trait.

Animals vary in masking traits that decrease the reliability of social learning. Social learning can be degraded by falsely presenting information to mislead others (deception) and suppressing information so as to not be detected (camouflage) (Stevens 2013). Masking strategies can also include concealment, misdirection, or distraction (often overlapping with tactical deception strategies; Whiten and Byrne 1988). For instance, pigs (*Sus domesticus*) that know the location of food employ tactics such as foraging at the least desirable food patches first and increasing foraging speed to reduce learning by naive competitors (Held et al. 2002, 2010). These behaviours aimed at deceiving competitors are masking traits. Masking may also require sophisticated social cognition, such

as assessing what competitors know and to which competitors one is vulnerable. For example, chimpanzees (*Pan troglodytes*) preferentially retrieve hidden food when competitors are misinformed or naive, rather than knowledgeable and likely to retaliate (Hare et al. 2001).

Our model of learning includes the simplifying assumption that selection on asocial learning, social learning and sending are mechanistically independent; although in nature, there could be interactions among traits influencing learning. For example, improvements in the capacities for encoding information might make an animal better at learning both asocially and socially (Heyes 2012). Alternatively, learning traits may trade off against each other, such as if time spent learning socially comes at the expense of learning asocially (Giraldeau et al. 2002). Further, competence may depend on combining asocial and social learning, with social learning leading animals to recognise a new behaviour before asocial learning refines the skills of performance (Galef 1995; Truskanov and Prat 2018; Kuijper et al. 2021). We focus on the mechanistically independent case, and assume learning traits are uncorrelated; this greatly simplifies the analysis in order to make initial predictions (Leimar 2009; Brown and Taylor 2010; Lehmann and Rousset 2014). Furthermore, the degree to which social and asocial learning mechanisms overlap remains an ongoing debate; overlap may be produced by a complicated interaction of the strength of selection produced by each domain, and how lower-level mechanisms are called on (Varela et al. 2020). Our focus is on the evolutionary conditions that influence investment in traits that impact learning, and other than assuming their mechanistic independence, we are agnostic as to the mechanisms that bring about changes to learning. That is, our model is compatible with a range of changes to cognitive or sensory systems, and morphology.

Social learning as cooperation

As social learning affects the fitness of both sender and receiver, the tools of social evolutionary theory can allow a greater understanding of learning traits. Although cooperation often entails an actor directly helping a recipient (e.g. sharing food), the same evolutionary logic applies when an actor provides information that facilitates learning a beneficial behaviour (e.g. the knowledge of how to find food). The fitness resulting from a cooperative behaviour can be partitioned into direct and indirect components (Hamilton 1964; Lehmann and Keller 2006; West et al. 2007). First, cooperative behaviour directly impacts the reproduction of the actor performing the behaviour (e.g. it may be costly to share food). Secondly, cooperative behaviour affects the reproduction of the recipient (e.g. it is beneficial to be given food), which produces indirect selection on the cooperative behaviour, to the degree that the actor and recipient are related. Hamilton's rule shows that cooperative behaviours

are selected when either the actor gets a direct benefit or, if the actor suffers a direct cost, the indirect benefit of helping relatives outweighs this cost (Hamilton 1964).

While the receiver will benefit from socially learning a productive new behaviour, the effect on the sender will vary. Learning may often impose a direct cost on the sender, because of a loss of advantage and increased competition. When senders experience direct costs from spreading information, social learning can only be beneficial for the sender if they are closely related to the receiver (Lehmann and Keller 2006; West et al. 2007). However, in other cases the sender may gain a direct advantage if synergy or reciprocation emerges through learning, so benefit in the absence of relatedness is possible (Lehmann and Keller 2006; West et al. 2007). For example, communal roosts may function as sites where animals reciprocally benefit from exchanging information about food and predators regardless of relatedness (Bijleveld et al. 2010; Evans et al. 2016). Particularly in the human case, receivers may even pay a direct cost in order to gain knowledge (Mesoudi 2008), which may be paid circuitously as the outcome of deference (Henrich and Gil-White 2001; Offord et al. 2019).

The degree to which both senders and receivers benefit from social learning should influence the joint evolution of learning traits (Hamilton 1964; Crawford and Sobel 1982; Giraldeau and Caraco 2000; Sterelny 2003; Danchin et al. 2004; Stevens 2013). When the sender suffers an overall cost from spreading the behaviour, the sender and receiver have *opposing interests*, and this could lead to a competitive evolutionary arms race between masking and social learning traits. Alternatively, if the sender gains an overall benefit when they are learned from, senders and receivers have *aligned interests*, which may lead to the joint evolution of teaching and social learning traits. Fundamentally, cooperative forms of social information involve both sender and receiver behaving in a predictable manner; whereas, antagonistic forms involve deception and being unpredictable (Owings and Morton 1997; Wolf et al. 2011; Dall and Griffith 2014).

Our model considers the evolution of masking of inadvertent social cues, which is different from deception occurring within a communication system. Traits selected to transmit information or *signals* evolve from unselected *inadvertent cues* when both sender and receiver benefit on average from the receiver's response (Searcy and Nowicki 2005; Danchin et al. 2008; Wagner and Danchin 2010; Stevens 2013; Magrath et al. 2015). Communication can evolve despite deception that exploits receivers by falsely producing signals, but this deception cannot be so costly that ignoring communication is more favourable (Maynard Smith and Harper 2003; Searcy and Nowicki 2005; Bradbury and Vehrencamp 2011). For instance, drongos (*Dicrurus adsimilis*) give enough honest alarm calls warning of predators so that babblers (*Turdoides*

bicolor) benefit by fleeing in response to calls, despite occasional deceptive alarms used to make babblers flee so their food can be stolen (Flower 2011). By contrast, the masking considered by our model occurs when the sender is always disadvantaged, so that sender and receiver have opposed interests over the long run. Indeed, when communication evolves with tolerated deception, sender and receiver still have aligned interests over the long run.

Metabolic costs of investing in learning traits

Traits for enhancing or reducing the reliability of learning are costly to build and maintain, consuming metabolic resources and time. Broadly, changes to information processing to increase cognitive capacities require metabolically expensive neural tissue (Sterling and Laughlin 2015). This means that more sophisticated learning traits that demand greater computation, or departure from usual activities, will be more metabolically expensive. For instance, masking that draws on higher cognition to outwit a competitor may be more metabolically expensive than masking that can be achieved by consuming food more rapidly. Any personal or cooperative benefits gained should outweigh these direct *metabolic costs* for learning trait evolution to be favoured. Complicated behaviours with many interrelated steps are inherently harder to learn, and upgrading cognition or spending time teaching will carry higher metabolic costs. Conversely, masking should be easier when a behaviour is complicated. Spatially spread-out or unstable social structures make observation of others more difficult, and populations where subordinate animals avoid dominant animals may also have weaker social transmission (Coussi-Korbel and Fragaszy 1995; Jones et al. 2017). Therefore, obtaining social information should carry high metabolic costs in diffuse groups, and masking should be cheaper. Adaptations to learning carry costs other than developing and maintaining neural tissue; as mentioned, both teaching and masking can involve the time cost of departing from the most efficient way of performing a behaviour. However, we use the term *metabolic cost* because it intuitively represents this suite of direct costs resulting from investing in traits that influence learning. Broadly, constraints on improving information should lead to higher metabolic costs for traits supporting learning, with constraints on degrading information leading to higher metabolic costs of masking.

Metabolic costs to improve learning traits may be paid to reduce the costs suffered during the process of learning. For instance, meerkats (*Suricata suricatta*) invest in teaching traits, whereby they spend time helping their young learn how to hunt scorpions. The metabolic costs of this teaching trait are worth paying when offset against the reduction in danger to their young, compared to unaided learning (Thornton 2008). The typical kinds of cost incurred during the process of learning have been hypothesised to differ between social and asocial learning (Boyd and Richerson 1985; Dall et al. 2005; Aplin 2016). In particular, learning asocially typically imposes time, energy or injury costs resulting from trial-and-error. Social learning saves these process costs by having others make the discovery, but can lead to errors due to social information being outdated or difficult for the receiver to use.

Model

We model a situation in which individuals gain benefits from learning a novel behaviour, but face costs or benefits if they are learned from; consequently, selection can favour investing in traits that influence the reliability of asocial and social learning. As our aim is to give a heuristic framework, we make few assumptions about how population structure affects the costs and benefits of learning, or relatedness (an issue we return to in the "Discussion" section). We start by focusing on the simplest case of a single bout of asocial learning followed by social learning, where being learned from leads to a localised cost or synergetic benefit for the sender. Further, we allow global competition costs or benefits that change the value of learned behaviour if a greater proportion of the population acquires the behaviour. Later, we extend to explore the effect of multiple bouts of social transmission leading to traditions of learned behaviour (Hoppitt and Laland 2013).

The success of learning is influenced by investment in metabolically costly traits for asocial learning, z, and social learning, x, as well as in traits for teaching or masking, y (Fig. 1). We call α and β the reliability of asocial and social learning, respectively, because they give the probability learning will be successful within an episode in which information is present. In particular, the reliability of asocial learning is an increasing function of investment in asocial learning traits, $\alpha(z)$, $\alpha \propto z$. The reliability of social learning is a function both of social learning traits of the receiver, and the traits of the sender who may teach or mask, $\beta(x, y)$.

There are two broad evolutionary relationships that are possible between traits of the sender and receiver. First, when there are aligned interests, receivers may invest to socially learn and senders may invest to teach, so both parties may improve the reliability of social learning. Secondly, when there are opposing interests, receivers may still invest to improve the reliability of social learning, but senders may invest to mask, and frustrate social learning. In particular, we assume the reliability of social learning is a piecewise function that obeys $\beta \propto x + y$ when there are aligned interests and $\beta \propto x - y$, when there are opposed

Fig. 1 Learning trait investment, the reliability of learning, and metabolic costs. The figure depicts the learning of capuchin monkeys, *Cebus capucinus*, about how to access edible seeds of the Panamá fruit (Barrett et al. 2017)

Learning traits for Asocial Learning

1. Animals invest *z* in traits for asocial learning, suffering metabolic cost $c_z \kappa(z)$, depending on trait sophistication
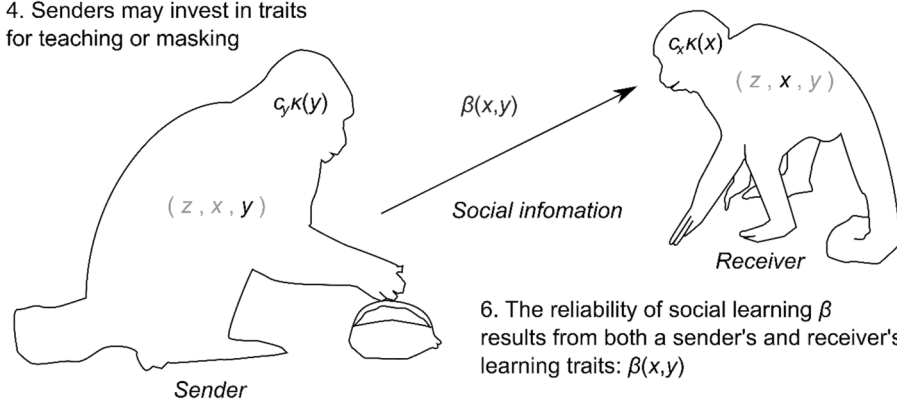
2. The reliability of asocial learning α improves with greater investment: $\alpha(z)$

$c_z \kappa(z)$

$\alpha(z)$
Personally acquired infomation

(z, x, y)
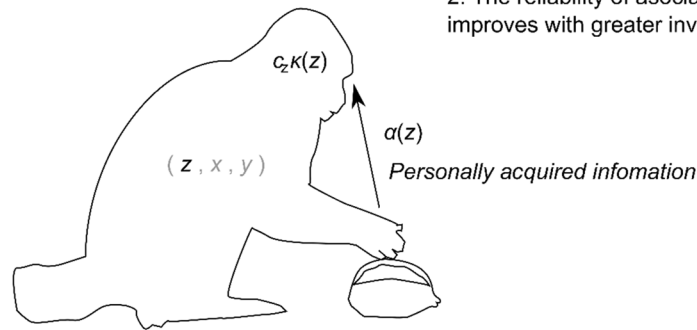
Learning traits for Social Learning

3. Senders invest *y* in traits affecting the production of social information at metabolic cost $c_y \kappa(y)$
Receivers invest *x* in social learning traits for using social information at metabolic cost $c_x \kappa(x)$

4. Senders may invest in traits for teaching or masking

$c_x \kappa(x)$

(z, x, y)

$c_y \kappa(y)$

$\beta(x,y)$

(z, x, y)

Social infomation

Receiver

6. The reliability of social learning β results from both a sender's and receiver's learning traits: $\beta(x,y)$

Sender

interests. That is, while we later give a formal condition for aligned versus opposed interests, in deriving this condition we examine two separate cases: sender investment either increases the reliability of social learning (teaching $\beta \propto x + y$) or decreases social learning (masking $\beta \propto x - y$). When there is no investment in sending or receiving traits, social learning only occurs on the basis of baseline inadvertent social information. We assume the metabolic costs of investing in each learning trait are independent and described by the same function κ, giving the extent of diminishing returns, as well as a linear parameter *c* describing the metabolic cost of that learning trait specifically (e.g. $c_x \kappa(x)$). To make progress in our analysis we assume particular functions relating investment to reliability and metabolic costs (Appendix 1).

We derive expected fitness *W* of a rare focal mutant with trait values (z, x, y) as follows (Eq. 1). We assume there is a best learnable behaviour in a changing environment, and if an animal learns that behaviour they acquire a benefit *b*. A focal mutant may learn the behaviour through asocial learning, gaining expected fitness $b\alpha(z)$. Alternatively, they may learn through social learning from another random member of the population, who themselves previously learned asocially. In this case, the mutant gains expected fitness $b(1 - \alpha(z))\alpha(\bar{z})\beta(x, \bar{y})$. In particular, $(1 - \alpha(z))$ is the probability the focal mutant did not learn asocially, $\alpha(\bar{z})$ is the proportion of the population that are potential senders (who carry the resident allele), and $\beta(x, \bar{y})$ is the reliability of social learning between a naive focal mutant and resident sender (conditional on an interaction).

$$
\begin{aligned}
W(z,x,y) = \underbrace{b}_{\substack{\text{acquiring}\\\text{benefit}}} & \left(\underbrace{\alpha(z)}_{\substack{\text{probability of}\\\text{asocial learning}}} + \underbrace{(1-\alpha(z))\alpha(\bar{z})\beta(x,\bar{y})}_{\substack{\text{probability of}\\\text{social learning}}} \right) \\
- \underbrace{a}_{\substack{\text{local}\\\text{competition cost}}} & \left(\underbrace{(1-\alpha(\bar{z}))\alpha(z)\beta(\bar{x},y)}_{\substack{\text{probability of}\\\text{being learned from}}} \right) \\
- \underbrace{d}_{\substack{\text{global}\\\text{competition cost}}} & \left(\underbrace{\alpha(\bar{z}) + (1-\alpha(\bar{z}))\alpha(\bar{z})\beta(\bar{x},\bar{y})}_{\substack{\text{probability of}\\\text{being learned from}}} \right) \\
- & \left(\underbrace{c_z\kappa(z) + c_x\kappa(x) + c_y\kappa(y)}_{\text{metabolic costs}} \right)
\end{aligned}
$$

$$(1)$$

The sender's fitness may change when they are learned from because of local interactions with the receiver, by an amount a. In the case of opposed interests, it may be that the receiver is able to immediately compete for a food-item the sender is consuming. In particular, if a is the severity of the cost, the focal mutant will pay an expected cost of being learned from of $a(1-\alpha(\bar{z}))\alpha(z)\beta(\bar{x},y)$. Alternatively, the sender may gain some local benefit when they are learned from; for example, if the receiver joins in mobbing a common predator. Here, there will be a local spreading benefit, such that $a < 0$.

Learning occurring anywhere in the population may affect the value of knowing a novel behaviour. For instance, resources can be scarce, so that when another group member learns how to exploit a food source, already knowledgeable members face a cost due to increased competition, regardless of if they were learned from personally. To study this form of density- and frequency-dependent selection, we have a focal mutant experience an increasing cost as the behaviour becomes more widespread. Let d be a global competition cost parameter, such that higher values represent more intense global competition (e.g. scarce resources). For simplicity, we assume d linearly weights the proportion of group members who know the behaviour: $d(\alpha(\bar{z}) + (1-\alpha(\bar{z}))\alpha(\bar{z})\beta(\bar{x},\bar{y}))$. This means that as a greater proportion of the population learns the behaviour the global competition costs are more severe, and the expected benefit of knowing the behaviour will be reduced. Furthermore, we also consider cases where group members gain synergistic benefits when others learn. For instance, predator detection will likely be more effective if group members know what predators look like. Here, there will be a global spreading benefit, such that $d < 0$.

The total metabolic cost of investing in learning traits is $-c_z\kappa(z)-c_x\kappa(x)-c_y\kappa(y)$. At the end of each generation, all individuals reproduce asexually and then die.

We assume mutants of small effect continually invade, rapidly becoming resident, and cause evolution in the sophistication of learning traits (Otto and Day 2007; Leimar 2009). However, selection on learning traits is complicated by the fact that relatives may interact. In order to access the coefficient of relatedness, r, we follow the method of Taylor and Frank (Taylor and Frank 1996; Brown and Taylor 2010; Gardner et al. 2011; Lehmann and Rousset 2014). This method takes the trait value of the resident who impacts the fitness of the mutant to be a function of the mutant's trait value $(\bar{z}(z), \bar{x}(x), \bar{y}(y))$. The coefficients of relatedness are automatically produced in deriving the fitness gradients for invasion by mutants, $\bar{z}'(z) = \bar{x}'(x) = \bar{y}'(y) = r$ (see Supplement; Gardner et al. 2011, p. 1036). Broadly, relatedness is the regression weight of a focal individual's trait value on those with whom it interacts (e.g. $r = \text{Cov}(\bar{x},x)/\text{Var}(x)$). Assuming the population is in the limit of vanishing trait variation this approaches the derivative of the interactor's trait value as a function of the focal mutant's trait value (e.g. $\text{Cov}(\bar{x},x)/\text{Var}(x) \to \bar{x}'(x)$). For reasons of simplicity, we assume the same relatedness for all traits (e.g. Brown and Taylor 2010). In fact, many processes producing relatedness, such as limited dispersal, act similarly on all traits, so this assumption is reasonably realistic. We find a single evolutionarily and convergently stable level of investment for each learning trait $(\hat{z}, \hat{x}, \hat{y})$ (Appendix 1).

Results

Condition for aligned interests

We uncover the fundamental condition necessary for there to be aligned interests, rather than opposed interests (inequality 2). If the learner always benefits, the consequences of being learned from for a sender dictate when interests are aligned. In particular, for aligned interests, the benefit conferred to the sender's relatives by acquiring the behaviour (br) must be larger than the sum of the global cost of knowledgeable relatives competing with each other (dr), and direct costs of local competition suffered by the sender personally (a):

$$(b-d)r - a > 0 \qquad (2)$$

This means that one way aligned interests can arise is if competition is weak and relatedness is high. Secondly, aligned interests may occur because synergy arises from learning ($a < 0$, $d < 0$). While inequality 2 dictates when senders gain revenue or a loss from producing information, it is not a sufficient condition for there to be investment in

teaching or masking. This is because for investment in any learning trait to be favoured, it is required that the revenue generated by changing learning is greater than the metabolic costs. Our results reveal when investing is profitable, considering that complicated relationships between traits affect their joint evolution. Here, we summarise insights produced by sensitivity analysis and the fitness gradients (presented in the Supplement).

Direct and indirect fitness effects

The personal consequences, and those for relatives, are different for investment in social learning compared with sending traits. We outline the primary direct and indirect fitness effects for social learning and sending traits in Fig. 2.

Inter-trait selection

Each learning trait influences the evolution of the others. The value of investing in traits for sending ($\hat{y}$) or social learning ($\hat{x}$) are most favoured when encounters between knowledgeable senders and naive receivers are likely (when

$(1 - \alpha(\hat{z}))\alpha(\hat{z})$ is large, maximised at $\alpha = 1/2$). This means the sophistication of traits involved with social learning explicitly depends on the investment in asocial learning traits. Improvements to asocial learning are primarily favoured if there are highly advantageous learnable behaviours and learning (asocially or socially) is currently unreliable ($(1 - \alpha\beta)$ is large). This means that the sophistication of asocial learning traits also explicitly depends on traits that affect social learning.

Relative investment in learning traits

In general, asocial learning attracts greater investment than social learning, which attracts greater investment than teaching or masking ($\hat{z} > \hat{x} > \hat{y}$). That is, while the absolute level of investment in each learning trait varies depending on relatedness and the costs and benefits of learning (b, a, d, r), the relative ordering of investment in learning traits is generally the same (Fig. 3). This ordering occurs because of inherent differences in expected revenue from investment

Fig. 2 The direct and indirect fitness consequences of learning for sending and receiving traits. Asocial learning traits are covered in the Supplement. Indirect selection occurs if learning takes place, because spreading the behaviour causes relatives to help or compete with each other. Metabolic costs are direct costs experienced unconditionally by individuals possessing sophisticated traits. Because metabolic costs influence learning they have circuitous social repercussions, but these effects are already accounted for in the coefficients of relatedness (r) that refer to the indirect selection produced by learning
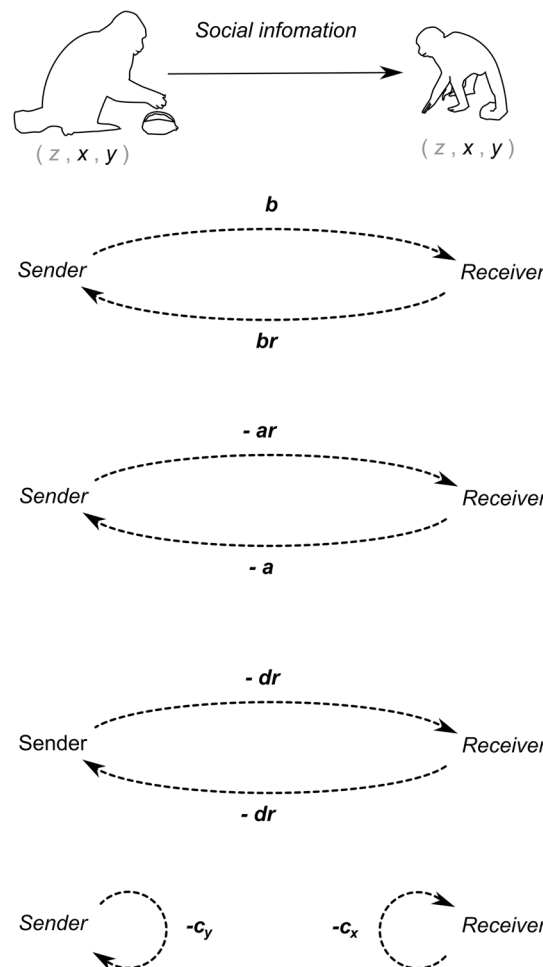
1. Social learning between kin
Both sender and receiver have genes for sending y and receiving x. Therefore, social learning leads to direct and indirect fitness consequences due to relatedness r.

2. Benefit of acquiring behaviour
The receiver gains a direct acquired benefit of learning b. The sender gains an indirect acquired benefit to the degree they are related to a receiver br.

3. Local consequences of learning
The sender suffers a direct cost $-a$, due to local competition with the receiver. The receiver suffers an indirect cost $-ar$ if they compete with a related sender. Alternatively, learning may lead to local synergy ($a < 0$): sender gains direct benefit, receiver indirect benefit.

4. Global consequences of learning
Competition may occur between any group members who learn, due to scare resources. Senders and receivers suffer a global competiton cost for contributing to competition with relatives dr. Alternatively, group-wide synergy may occur. Here, all gain a global spreading benefit, as relatives are helped ($d < 0$).
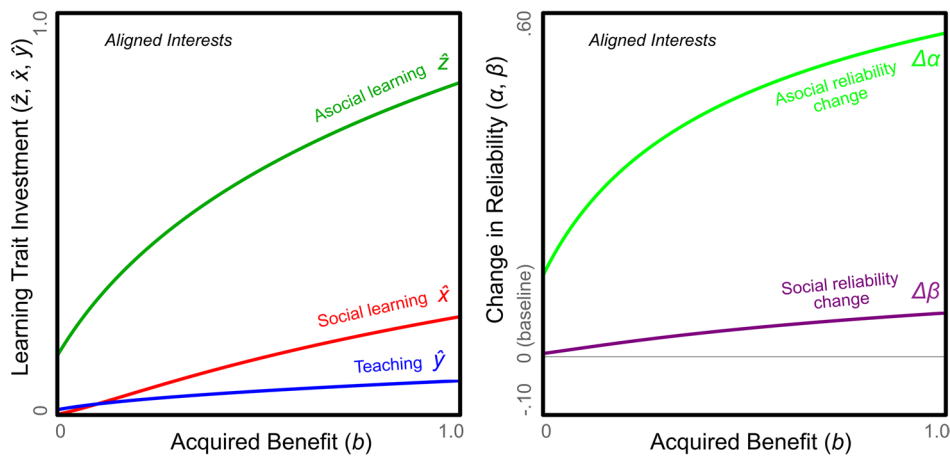
5. Metabolic costs of investment
Sender (c_y) and receiver (c_x) suffer direct metabolic costs for investing, regardless of if learning occurs.
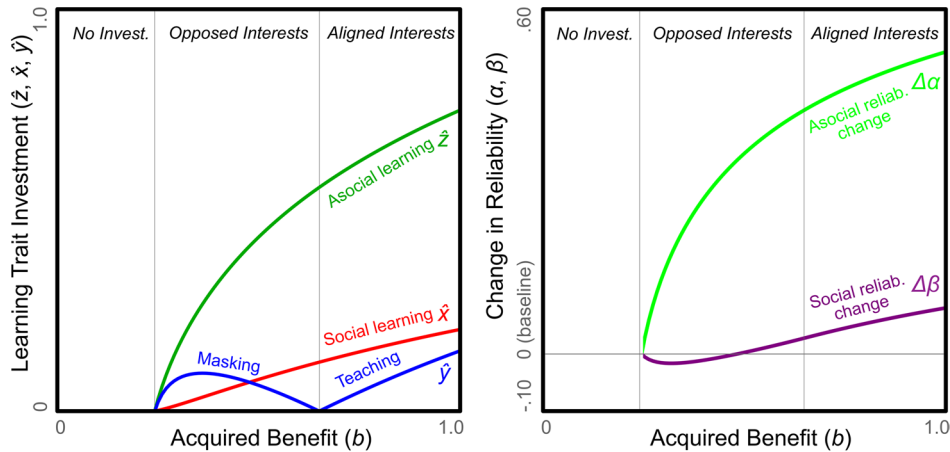
Fig. 3 Optimal learning trait investment and associated changes in the reliability of social and asocial learning. **A.** Evolution under sender-receiver competition ($a = 0.1, d = 0.4, r = 0.4, c_z = 0.4, c_x = 0.2, c_y = 0.03$) **B.** Evolution under sender-receiver synergy ($a = d = -0.1, r = c_z = c_x = c_y = 0.1$). Regions of aligned interests occur at combinations of parameters such that $(b - d)r - a > 0$. If $(b - d)r - a < 0$ then interests are opposed. Change in reliability is shown from the baseline provided by inadvertent cues, so that the change is negative (below baseline) when masking dominates social learning traits

in learning traits unless there are substantial counteracting differences in their metabolic costs (Fig. 2).

Asocial learning may generally attract greater investment than social learning traits, because asocial learning is less contingent on the behaviour of others. Investment to make asocial learning more likely will pay off if an animal is unlikely to learn the behaviour at their current level of investment, regardless of whether this is because social or asocial learning is unreliable ($1 - \alpha\beta = (1 - \alpha) + (1 - \beta)\alpha$). By comparison, a beneficial investment in social learning requires that an animal must be both unlikely to learn asocially and likely to encounter a knowledgeable sender ($(1 - \alpha)\alpha$, which is always less likely).

Social learning traits generally attract greater investment than teaching, because the receiver usually profits more from learning a behaviour than the sender does from spreading the behaviour. While the receiver gains the full benefit of acquiring a novel behaviour, the sender only benefits when they teach a related receiver ($b > br$). Further, the sender always suffers the full cost of local competition when they are learned from (a), whereas the receiver only suffers when they compete with a related sender ($a > ar$). Similarly, investing in traits for receiving generally leads to greater profit than masking. This is because the benefit for a naive animal of acquiring information may often be greater than losing a share of those benefits for a knowledgeable sender ($b > a$) (consider competition over food). Furthermore, masking incurs a larger cost by preventing relatives from learning, than receiving does by causing competition with related senders ($br > ar$ if $b > a$).

Reliability due to consequences of learning

We now examine how the consequences of the spread of a behaviour affects the reliability of learning under the conditions of competition (Fig. 3A) and synergy (Fig. 3B); extreme circumstances are presented in the Appendix 2. Our main results can be understood by examining how reliability changes with the benefits of acquiring the behaviour (b). This is because the effects of reducing acquired benefits are analogous to increasing competition (a, d).

Competition Even when there is competition, if the learner gains large benefits from acquiring information then both social and asocial learning will be highly reliable, because there is selection for greater investment in traits that support learning (Fig. 3A). At the other extreme, if acquired benefits are negligible then there is no incentive to learn, and therefore no behaviours enter the population via asocial learning to allow social learning. Consequently, there is no investment in any learning trait.

Masking is selected when the benefits acquired by learning are low relative to competition, but competition cannot be so strong as to cancel any advantages of acquiring the behaviour. Competition not only erodes the benefit of the sender, but also receivers and asocial learners, who by learning may compete with relatives (Fig. 2). Further, learning is unproductive if in the future you will likely become a sender who faces strong competition. The conditions for masking exist when competition is strong enough to make it worthwhile for senders to obscure information, but competition is still weak enough that learning the behaviour is still beneficial. In particular, we predict that local competition, occurring between sender and receiver, often selects for masking, rather than global competition over scarce resources. This is because global competition equally affects sender and receiver, so discourages overall investment in learning. By contrast, local competition produces greater costs for the sender (direct) than the receiver (indirect) (Fig. 2.). Therefore, local competition leads to a greater incentive for obscuring information for the sender, while still retaining benefits for receiving.

As acquired benefits become larger compared to competition, so too do the indirect fitness benefits of helping relatives learn, causing divestment in masking. When acquired benefits are larger than competition costs (aligned interests), there is investment towards teaching.

Synergy If there is synergy as a result of learning, then there is greater incentive to invest in traits supporting learning, so that learning is highly reliable (Fig. 3B). This is because senders gain a direct advantage, with their use of a behaviour gaining value when they are learned from. Further, in addition to acquiring the behaviour itself, learning provides the bonus of helping relatives, rather than eroding benefits through competition. This means that higher relatedness increases investment in traits supporting learning.

Metabolic costs

Higher metabolic costs cause divestment in a given learning trait, and this has flow-on effects, redistributing investment in other traits. Intermediate costs of investing in asocial learning (c_z) increases selection on sending and receiving traits, because there will be greater variation in whether individuals learn asocially, resulting in a higher chance of an encounter leading to social learning. High costs lead to there being few asocial learners, and low costs lead to most group members learning asocially. Increasing the cost of social learning traits (c_x), decreases the probability of social learning, and this generally increases investment in asocial learning. Similarly, increased costs of sending traits (c_y) reduce investment in teaching or masking traits, and so make social learning either less or more reliable, respectively. In general, asocial learning will gain greater investment when costs of sending are such that social learning is unreliable. The costs of social learning traits have little effect on sending trait investment or vice versa, due to our simple assumption that their effect on social learning is additive (we discuss alternatives in the Supplement).

Multiple learning opportunities

Although we have been modelling a single episode of learning, often in nature behaviours are transmitted over multiple bouts of social learning, resulting in traditions. Within the structure of the current model, considering multiple bouts of learning greatly complicates the analysis; however, to explore this possibility we consider a second bout of asocial and social learning. The equations are cumbersome and are provided in the Supplement. In the two-bout model, the general pattern of selection on learning traits is the same, as is the relative ordering of investment in traits ($\hat{z} > \hat{x} > \hat{y}$). However, the absolute investment in all traits for improving learning is reduced. This is because repeated bouts of learning still allow the behaviour to be acquired, even when the probability of learning in any single bout is low. The exception is masking, which is more valuable when there are multiple attempts to learn from senders, and so attracts greater investment.

There is overall consistency with the one-bout learning model, despite the fact there are more complicated flow-on effects of investment in social learning. For instance, in the two-bout model, social learning trait investment is impacted not only by the increased chance of socially acquiring the behaviour oneself, but also by the fact that those who learn socially may then spread the behaviour to relatives. There is also consistency with previous studies that confirm that unreliable learning,

when ratcheted over several bouts, still allows learnable behaviour to be retained in the population (McElreath et al. 2018).

Discussion

We investigated the joint evolution of learning traits, to aid in understanding why reliable social learning occurs in some animals but not others. In summary, we identified several pressures that generally select for reliable social learning: (1) large benefits from learned behaviour; (2) receivers directly help the sender (or at least are not in strong competition); (3) population-wide spreading of learned behaviour provides synergistic benefits (or leads to little global competition); (4) a high degree of relatedness; (5) improving traits for social learning is cheap; (6) masking adaptations are expensive; and (7) improving traits for asocial learning is moderately costly. Further, we found that asocial learning traits should often be more sophisticated than traits for receiving, with receiving traits being more sophisticated than traits of the sender for teaching or masking. Our model finds that sophisticated traits for affecting social learning occur both when there are aligned and opposed interests. That is, both extremes of the continuum can produce conditions that make it advantageous to invest in metabolically expensive traits to influence social learning. However, aligned interests lead to traits designed to support learning, whereas opposed interests lead to a conflict between masking and social learning traits.

For sender and receiver to have aligned interests, the sender must gain a net indirect benefit of helping a relative learn that is larger than the direct costs of competing with the receiver ($(b - d)r - a > 0$). Here, the net indirect benefit is fitness gained by helping relatives learn, discounted by the increased competition between relatives. Therefore, we discover a condition that fundamentally determines whether learning traits will be complementary (aligned interests) or antagonistic (opposed interests).

Our formal condition for aligned or opposing interests links Hamilton's classification of social behaviours (Hamilton 1964) with that of social information use (Giraldeau and Caraco 2000; Sterelny 2003; Danchin et al. 2004; Stevens 2013). In particular, aligned interests are an informational form of *altruism*, if the indirect benefits of helping a relative learn are larger than the direct costs of teaching ($(b - d)r - a > 0$ and $a > 0$); (Hoppitt et al. 2008; Thornton and Raihani 2008; Fogarty et al. 2011). Alternatively, aligned interests are informational *mutualism*, if the sender gains a sufficient direct benefit by being learned from, via synergy or reciprocation ($(b - d)r - a > 0$ and $a < 0$). However, there are opposing interests if the costs of spreading the behaviour are sufficiently large to the sender, so that learning is informational *parasitism* or *scrounging* ($(b - d)r - a < 0$). We predict that most instances of informational parasitism occur because the sender suffers personally from competition when they are learned from, such as in kleptoparasitism. Density dependent competition among relatives expands the conditions for informational parasitism, but when global competition is too intense any adaptations affecting learning are pointless.

Our work highlights that instances of social learning can be placed on a social evolutionary continuum; at one extreme, senders gain large benefits from aiding receivers by teaching; at the other extreme, senders suffer substantial costs when they are learned from, so attempt to mask. However, selection may often prioritise capacities for asocial and social learning over teaching and masking. Consequently, many species may occupy the middle of the continuum, even considering that sophisticated teaching is underreported (Thornton and Raihani 2010), with masking being even less well studied.

Broadly, intelligence is often hypothesised to result from one of two pressures due to social life: (1) an arms race between Machiavellian competitors attempting to exploit each other, or (2) the challenges of coordinating and sharing information (Sterelny 2007; Kendal 2011). We find that either of these hypotheses can explain the evolution of sophisticated learning traits, depending on the consequences of spreading the behaviour, degree of relatedness, and ease of social transmission. To illustrate by example, compare meerkats, who have complementary adaptations, to western scrub-jays (*Aphelocoma californica*), who have antagonistic adaptations. Both species live in demanding environments in which learned behaviours are highly valuable, and both are often successful when learning novel tasks (Clayton et al. 2007; Thornton and Clutton-Brock 2011; Thornton and Samson 2012). This agrees with our finding that overwhelmingly valuable behaviours lead to coupled investment in social and asocial learning traits, and aligns with the view that some animals enter a learning-based niche, so that capacities for social and asocial learning are correlated (Reader and Laland 2002; Laland 2017). Unlike western scrub-jays, meerkats are obligate cooperative breeders who live in highly social groups of up to 40, many of whom are siblings or half-siblings (Clutton-Brock et al. 2001; Griffin et al. 2003). This is a context of high relatedness and cheap transmission of social information. As our model predicts, meerkats have evolved teaching, including moderating the difficulty of *lessons* depending on the abilities of the receiver (Thornton and McAuliffe 2006). Conversely, western scrub-jays form territorial pair-bonds with occasional associations with others (Curry et al. 2002; Clayton et al. 2007), and so masking social information should be cheap. As western scrub-jays live in seasonally resource-poor environments, there is also strong competition for food, and spreading information is often locally (personally) costly. As our model predicts, western

scrub-jays are sophisticated maskers who track competitors to whom they are vulnerable, and cache food in ways that account for what competitors can observe (Clayton et al. 2007; Grodzinski and Clayton 2010).

Synergy resulting from learning can lead to strong selection for reliable social learning, even in the absence of relatedness. Because learning leads the sender to gain a further fitness bonus when there is synergy, we predict greater investment in capacities for social learning. An example of this may be fairy-wrens (*Malurus cyaneus*), who socially learn to identify threatening brood parasites, improving overall vigilance (Feeney and Langmore 2013); however, sender and receiver are frequently unrelated (Mulder et al. 1994). Such social learning could also occur among heterospecifics that learn to recognise alarm calls to reduce personal risk of predation (Magrath et al. 2015, 2020). When synergies arise from learning, high relatedness has a reinforcing effect on the reliability of social learning. This is because receivers help both related senders and other relatives in the group, rather than competing with them.

The current model highlights that senders evolve in response to receiver strategies, which may moderate the conclusions of previous social learning theory. Much previous research has studied social learning strategies for using social information to acquire favourable behaviours (Laland 2004; Rendell et al. 2011; Kendal et al. 2018). Important strategies include preferentially learning from successful, dominant or prestigious individuals; switching to asocial learning when social learning is unsuccessful; or copying behaviours that are more frequently used in the population. We deal with the simplified scenario of random interaction between pairs of senders and receivers, which is different from the assumption of strategic partner choice and use of multiple partners, underpinning many social learning strategies. Nonetheless, our model suggests senders can evolve to counter or facilitate the effectiveness of social learning strategies, which are typically thought of as strategies of the receiver.

It is important to consider the constraints on using information to understand when learning traits will become sophisticated. A learning trait cannot become sophisticated when there are substantial metabolic costs that constrain using or producing information. This means the transmission and processing of information must be considered alongside the fitness consequences of learning. For instance, sophisticated teaching may require all the cognitive capacities to learn the behaviour in the first place (as a receiver), but additional capacities to provide information to a receiver. Teaching would therefore have inherently higher metabolic costs limiting its sophistication. Furthermore, metabolic costs for a given learning trait have flow-on effects for other learning traits, in ways that sometimes defy expectation. For instance, divestment from asocial learning occurs if it has high metabolic costs, but this does not always lead to greater investment in social learning. This is because a decrease in the probability of asocial learning reduces the number of senders, so reduces the expected benefit of investing in social learning.

Our model could form the basis of further work exploring the effects of different social structures. Heuristics are useful in guiding thought, but can fail under particular circumstances. Here, our aim was generality, and to delineate sources of direct and indirect fitness on traits involved with learning (b, a, d, c). Consequently, we treat most details of population structure and dynamics as exogenous, making strong simplifying assumptions and giving few specifics. This means models making more explicit and realistic assumptions are likely to find that only specific combinations of our parameters will be allowable.

In nature, many more dynamics exist that would greatly complicate our analysis. For instance, animals can form temporary groups and move between patches depending on productivity, affecting group composition and competition (Giraldeau and Caraco 2000; Giraldeau and Dubois 2008; Afshar and Giraldeau 2014; Aoki and Feldman 2014). Although our inclusion of these issues in our model was simplistic, it did highlight the need to consider frequency and density dependence alongside social learning evolution. Notably, many important instances of social learning lead to culture that is transmitted between generations (Cavalli-Sforza and Feldman 1981; Hoppitt and Laland 2013). Population density and the value of culture interact; for instance, more useful behaviours may be discovered when there are many innovators, and valuable behaviours are less likely to be lost (Henrich 2004; Powell et al. 2009; Muthukrishna and Henrich 2016; Cantor et al. 2020). Further, animal populations may contain dominance hierarchies and have social structure that constrain the transmission of behaviours; complicating matters further, the spreading of behaviours may restructure social networks as group members benefit from occupying similar or different niches (Coussi-Korbel and Fragaszy 1995; Giraldeau and Caraco 2000; Aplin et al. 2015; Turner and Flynn 2016; Jones et al. 2017). In natural populations, not all members can acquire all behaviours, so group members must adopt different strategies (Dall and Griffith 2014; Barrett et al. 2017; Jones et al. 2017).

We found that teaching gives rise to a trade-off that affects altruism more broadly. Namely, helping relatives learn gives them a benefit, but this benefit is reduced when learning spreads because kin come to compete with each other (Taylor 1992; West et al. 2002). Indeed, specific assumptions about population dynamics can lead to kin benefits and competition cancelling each other out (Taylor 1992). Nonetheless, a range of models with more realistic assumptions find that altruism can often evolve despite competition between kin (Whitlock and Van Dyken 2011). Social learning is a particularly important

domain in which to consider such a trade-off because it is also a transmission mechanism, enabling behaviours to rapidly spread, which can cause relatives to compete over resources.

Cumulative culture allows an important form of synergistic benefit to arise. In particular, when social learning becomes sufficiently reliable, learnable behaviours may acquire advantageous modification and increase in value over generations (Sterelny 2007; Muthukrishna and Henrich 2016; Laland 2017; Mesoudi and Thornton 2018; Whiten 2019). This in turn increases the benefits of investing in learning, and so causes a feedback loop that may have led to the evolution of the highly sophisticated learning traits and culture seen in humans.

Appendix 1. Equilibrium and stability

Broadly, we assume changes in the reliability of learning monotonically increase with investment, but can never be perfect (equal 1). Further, we assume that increases in investment lead to diminishing returns. The existence of a single equilibrium, as well as key results about how learning evolves, can be proven making only these weak assumptions (Supplement). However, no closed form solution for this equilibrium can be produced, so we also relied on numerical methods. High-order derivatives were examined by sensitivity analysis that support that this equilibrium is convergent and evolutionarily stable over a broad range of parameter combinations. In particular, we used the following functions for the reliability of asocial and social learning, respectively:

$$\alpha(z) = 1 - \mathrm{e}^{-z} \tag{3}$$

$$\beta(x,y) = \begin{cases} 1 - \frac{1}{4}\mathrm{e}^{-x} - \frac{1}{4}\mathrm{e}^{-y}, & (b-d)r - a > 0 \\ \frac{1}{2} - \frac{1}{4}\mathrm{e}^{-x} + \frac{1}{4}\mathrm{e}^{-y}, & (b-d)r - a < 0 \end{cases} \tag{4}$$

Here, the baseline reliability of social learning is 0.5. Furthermore, to adhere to our assumptions of diminishing returns, we assume metabolic costs escalate with investment according to:

$$\kappa(i) = i^2 \quad \text{where } i \in \{z, x, y\} \tag{5}$$

Appendix 2. Findings under extreme conditions

Very strong synergy accompanied by high relatedness can lead to a reduction in investment in asocial learning (rather than an increase). In particular, synergy must provide larger benefits than acquiring the behaviour in the first place. This exception occurs because asocial learning avoids synergy

between relatives; it becomes better to wait to be helped. By corollary, intense local competition accompanied by high relatedness can lead to investment in asocial learning, as a way of preventing competition between relatives due to social learning.

High benefits of acquiring a novel behaviour can select against teaching when relatedness is negligible (rather than supporting it). This exception occurs when acquired benefits are large, because selection will favour the population to contain many highly effective asocial learners, reducing the need for teaching.

Declarations

References

Afshar M, Giraldeau L-A (2014) A unified modelling approach for producer–scrounger games in complex ecological conditions. Anim Behav 96:167–176. https://doi.org/10.1016/j.anbehav.2014.07.022

Aoki K, Feldman MW (2014) Evolution of learning strategies in temporally and spatially variable environments: a review of theory. Theor Pop Biol 91:3–19. https://doi.org/10.1016/j.tpb.2013.10.004

Aplin LM (2016) Understanding the multiple factors governing social learning and the diffusion of innovations. Curr Opin Behav Sci 12:59–65. https://doi.org/10.1016/j.cobeha.2016.09.003

Aplin LM (2019) Culture and cultural evolution in birds: a review of the evidence. Anim Behav 147:179–187. https://doi.org/10.1016/j.anbehav.2018.05.001

Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon B (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518:538–541. https://doi.org/10.1038/nature13998

Barnard CJ, Sibly RM (1981) Producers and scroungers: a general model and its application to captive flocks of house sparrows. Anim Behav 29:543–550. https://doi.org/10.1016/S0003-3472(81)80117-0

Barrett BJ, McElreath RL, Perry SE (2017) Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. Proc R Soc B 284:20170358. https://doi.org/10.1098/rspb.2017.0358

Bijleveld AI, Egas M, van Gils JA, Piersma T (2010) Beyond the information centre hypothesis: communal roosting for information on food, predators, travel companions and mates? Oikos 119:277–285. https://doi.org/10.1111/j.1600-0706.2009.17892.x

Boyd R, Richerson PJ (1985) Culture and the evolutionary process. University of Chicago Press, Chicago

Boyd R, Richerson PJ, Henrich J (2011) The cultural niche: why social learning is essential for human adaptation. P Natl Acad Sci USA 108(Suppl 2):10918–10925. https://doi.org/10.1073/pnas.1100290108

Bradbury JW, Vehrencamp SL (2011) Principles of Animal Communication, 2nd edn. Macmillan Education, London

Brown SP, Taylor PD (2010) Joint evolution of multiple social traits: a kin selection analysis. Proc R Soc Lond B 277:415–422. https://doi.org/10.1098/rspb.2009.1480

Byrne RW, Whiten A (1985) Tactical deception of familiar individuals in baboons (*Papio ursinus*). Anim Behav 33:669–673. https://doi.org/10.1016/S0003-3472(85)80093-2

Cantor M, Aplin LM, Farine DR (2020) A primer on the relationship between group size and group performance. Anim Behav 166:139–146. https://doi.org/10.1016/j.anbehav.2020.06.017

Cavalli-Sforza LL, Feldman MW (1981) Cultural Transmission and Evolution: A Quantitative Approach. Princeton University Press, Princeton

Chimento M, Barrett BJ, Kandler A, Aplin LM (2022) Cultural diffusion dynamics depend on behavioural productions rules. Proc R Soc B 289:20221001. https://doi.org/10.1098/rspb.2022.1001

Clarke JA (2010) White-tailed ptarmigan food calls enhance chick diet choice: learning nutritional wisdom? Anim Behav 79:25–30. https://doi.org/10.1016/j.anbehav.2009.09.021

Clayton NS, Dally JM, Emery NJ (2007) Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. Phil Trans R Soc B 362:507–522. https://doi.org/10.1098/rstb.2006.1992

Clutton-Brock TH, Brotherton PN, Russell AF et al (2001) Cooperation, control, and concession in meerkat groups. Science 291:478–481. https://doi.org/10.1126/science.291.5503.478

Coussi-Korbel S, Fragaszy DM (1995) On the relation between social dynamics and social learning. Anim Behav 50:1441–1453. https://doi.org/10.1016/0003-3472(95)80001-8

Crawford VP, Sobel J (1982) Strategic information transmission. Econometrica 50:1431–1451. https://doi.org/10.2307/1913390

Curry R, Townsend Peterson A, Langen T (2002) Western scrub-jay. In: Pool A, Gill F (eds) The birds of North America. American Ornithologists Union, Washington, pp 1–36

Dall SRX, Griffith S (2014) An empiricist guide to animal personality variation in ecology and evolution. Front Ecol Evo 2:3. https://doi.org/10.3389/fevo.2014.00003

Dall SRX, Giraldeau L-A, Olsson O, McNamara J, Stephens DW (2005) Information and its use by animals in evolutionary ecology. Trends Ecol Evol 20:187–193. https://doi.org/10.3389/fevo.2014.00003

Danchin É, Giraldeau L-A, Valone TJ, Wagner RH (2004) Public information: From nosy neighbors to cultural evolution. Science 305:487–491. https://doi.org/10.1126/science.1098254

Danchin É, Giraldeau L-A, Wagner RH (2008) An information-driven approach to behaviour. In: Danchin É, Giraldeau L-A, Cézilly F (eds) Behavioural Ecology. Oxford University Press, New York, pp 97–130

Donato DB, Potts RT (2004) Culturally transmitted predation and consumption techniques by Torresian Crows *Corvus orru* on Cane Toads *Bufo marinus*. Aust Field Ornithol 21:125–126

Evans JC, Votier SC, Dall SRX (2016) Information use in colonial living. Biol Rev 91:658–672. https://doi.org/10.1111/brv.12188

Feeney WE, Langmore NE (2013) Social learning of a brood parasite by its host. Biol Lett 9:20130443. https://doi.org/10.1098/rsbl.2013.0443

Flower T (2011) Fork-tailed drongos use deceptive mimicked alarm calls to steal food. Proc R Soc Lond B 278:1548–1555. https://doi.org/10.1098/rspb.2010.1932

Fogarty L, Strimling P, Laland KN (2011) The evolution of teaching. Evolution 65:2760–2770. https://doi.org/10.1016/j.anbehav.2007.12.014

Galef BG Jr (1995) Why behaviour patterns that animals learn socially are locally adaptive. Anim Behav 49:1325–1334. https://doi.org/10.1006/anbe.1995.0164

Gardner A, West SA, Wild G (2011) The genetical theory of kin selection. J Evol Biol 24:1020–1043. https://doi.org/10.1111/j.1420-9101.2011.02236.x

Giraldeau L-A, Caraco T (2000) Social foraging theory. Princeton University Press, Princeton

Giraldeau L-A, Dubois F (2008) Social foraging and the study of exploitative behavior. Adv Stud Behav 38:59–104. https://doi.org/10.1016/S0065-3454(08)00002-8

Giraldeau L-A, Valone TJ, Templeton JJ (2002) Potential disadvantages of using socially acquired information. Phil Trans R Soc B 357:1559–1566. https://doi.org/10.1098/rstb.2002.1065

Griffin AS, Pemberton JM, Brotherton PNM et al (2003) A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). Behav Ecol 14:472–480. https://doi.org/10.1093/beheco/arg040

Grodzinski U, Clayton NS (2010) Problems faced by food-caching corvids and the evolution of cognitive solutions. Phil Trans R Soc B 365:977–987. https://doi.org/10.1098/rstb.2009.0210

Hackett S, Ruxton GD, Schaefer HM (2016) Investment in attending to cues and the evolution of amplifiers. J Evol Biol 29:1131–1141. https://doi.org/10.1111/jeb.12853

Hamilton WD (1964) The genetic theory of social behavior. I and II. J Theor Biol 7:1–52. https://doi.org/10.1016/0022-5193(64)90038-4

Hare B, Call J, Tomasello M (2001) Do chimpanzees know what conspecifics know? Anim Behav 61:139–151. https://doi.org/10.1006/anbe.1999.1377

Held SDE, Mendl MT, Devereux C, Byrne RW (2002) Foraging pigs alter their behaviour in response to exploitation. Anim Behav 64:157–165. https://doi.org/10.1006/anbe.2002.3044

Held SDE, Byrne RW, Jones S, Murphy E, Friel M, Mendl MT (2010) Domestic pigs, *Sus scrofa*, adjust their foraging behaviour to whom they are foraging with. Anim Behav 79:857–862. https://doi.org/10.1016/j.anbehav.2009.12.035

Henrich J (2015) The secret of our success. Princeton University Press, Princeton

Henrich J (2004) Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses—the Tasmanian case. Am Antiq 69:197–214. https://doi.org/10.2307/4128416

Henrich J, Gil-White FJ (2001) The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. Evol Hum Behav 22:165–196. https://doi.org/10.1016/S1090-5138(00)00071-4

Heyes C (1994) Social learning in animals: categories and mechanisms. Biol Rev 69:207–231. https://doi.org/10.1111/j.1469-185X.1994.tb01506.x

Heyes C (2012) What's social about social learning? J Comp Psychol 126:193–202. https://doi.org/10.1037/a0025180

Hoppitt W, Laland KN (2013) Social learning: An introduction to mechanisms, methods, and models. Princeton University Press, Princeton

Hoppitt WJE, Brown GR, Kendal R, Rendell L, Thornton A, Webster M, Laland K (2008) Lessons from animal teaching. Trends Ecol Evol 23:486–493. https://doi.org/10.1016/j.tree.2008.05.008

Jones TB, Aplin LM, Devost I, Morand-Ferron J (2017) Individual and ecological determinants of social information transmission in the wild. Anim Behav 129:93–101. https://doi.org/10.1016/j.anbehav.2017.05.011

Kendal JR (2011) Interactions between cognition and culture. In: Swami V (ed) Evolutionary psychology: a critical introduction. Wiley-Blackwell, Oxford, pp 311–342

Kendal RL, Boogert NJ, Rendell L, Laland K, Webster M, Jones PL (2018) Social learning strategies: bridge-building between fields. Trends Cogn Sci 22:651–665. https://doi.org/10.1016/j.tics.2018.04.003

Kuijper B, Leimar O, Hammerstein P, McNamara J, Dall SRX (2021) The evolution of social learning as phenotypic cue integration. Phil Trans R Soc B 376:20200048. https://doi.org/10.1098/rstb.2020.0048

Laland KN (2004) Social learning strategies. Anim Learn Behav 32:4–14. https://doi.org/10.3758/BF03196002

Laland KN (2017) Darwin's unfinished symphony: how culture made the human mind. Princeton University Press, Princeton

Laland KN, Kendal JR (2003) What the models say about social learning. In: Fragaszy D, Perry S (eds) The biology of traditions: Models and evidence. Cambridge University Press, Cambridge, pp 33–55

Laland KN, Atton N, Webster MM (2011) From fish to fashion: experimental and theoretical insights into the evolution of culture. Phil Trans R Soc B 366:958–968. https://doi.org/10.1098/rstb.2010.0328

Lehmann L, Keller L (2006) The evolution of cooperation and altruism–a general framework and a classification of models. J Evol Biol 19:1365–1376. https://doi.org/10.1111/j.1420-9101.2006.01119.x

Lehmann L, Rousset F (2014) The genetical theory of social behaviour. Phil Trans R Soc B 369:20130357. https://doi.org/10.1098/rstb.2013.0357

Leimar O (2009) Multidimensional convergence stability. Evol Ecol Res 11:191–208

Magrath RD, Haff TM, Fallow PM, Radford AN (2015) Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biol Rev 90:560–586. https://doi.org/10.1111/brv.12122

Magrath RD, Haff TM, Igic B (2020) Interspecific communication: gaining information from heterospecific alarm calls. In: Aubin T, Mathevon N (eds) Coding strategies in vertebrate acoustic communication. Springer International Publishing, Cham, pp 287–314

Maynard Smith J, Harper D (2003) Animal signals. Oxford University Press, Oxford

Mcelreath MB, Boesch C, Kühl H, McElreath R (2018) Complex dynamics from simple cognition: The primary ratchet effect in animal culture. Evol Behav Sci 12:191–202. https://doi.org/10.1037/ebs0000117

Mesoudi A (2008) An experimental simulation of the "copy-successful-individuals" cultural learning strategy: adaptive landscapes, producer–scrounger dynamics, and informational access costs. Evol Hum Behav 29:350–363. https://doi.org/10.1016/j.evolhumbehav.2008.04.005

Mesoudi A, Thornton A (2018) What is cumulative cultural evolution? Proc R Soc B 285:20180712. https://doi.org/10.1098/rspb.2018.0712

Miller SE, Sheehan MJ, Reeve HK (2020) Coevolution of cognitive abilities and identity signals in individual recognition systems. Phil Trans R Soc B 375:20190467. https://doi.org/10.1098/rstb.2019.0467

Montrey M, Shultz TR (2020) The evolution of high-fidelity social learning. Proc R Soc B 287:20200090. https://doi.org/10.1098/rspb.2020.0090

Mulder RA, Dunn PO, Cockburn A, Lazenby Cohen KA, Howell MJ (1994) Helpers liberate female Fairy-wrens from constraints on extra-pair mate choice. Proc R Soc Lond B 255:223–229. https://doi.org/10.1098/rspb.1994.0032

Muthukrishna M, Henrich J (2016) Innovation in the collective brain. Phil Trans R Soc B 371:20150192. https://doi.org/10.1098/rstb.2015.0192

Offord M, Gill R, Kendal J (2019) The effects of prestige on collective performance and information flow in a strictly hierarchical institution. Palgrave Commun 5:1–11. https://doi.org/10.1057/s41599-018-0211-8

Otto SP, Day T (2007) A biologist's guide to mathematical modeling in ecology and evolution. Princeton University Press, Princeton

Owings DH, Morton ES (1997) The role of information in communication: an assessment/management approach. Persp Ethol 12:359–390

Powell A, Shennan S, Thomas MG (2009) Late Pleistocene demography and the appearance of modern human behavior. Science 324:1298–1301. https://doi.org/10.1126/science.1170165

Reader SM, Laland KN (2002) Social intelligence, innovation, and enhanced brain size in primates. P Natl Acad Sci USA 99:4436–4441. https://doi.org/10.1073/pnas.062041299

Rendell L, Boyd R, Cownden D et al (2010) Why copy others? Insights from the social learning strategies tournament. Science 328:208–213. https://doi.org/10.1126/science.1184719

Rendell L, Fogarty L, Hoppitt WJE, Morgan TJH, Webster MW, Laland K (2011) Cognitive culture: theoretical and empirical insights into social learning strategies. Trends Cogn Sci 15:68–76. https://doi.org/10.1016/j.tics.2010.12.002

Rogers AR (1988) Does biology constrain culture? Am Anthropol 90:819–831. https://doi.org/10.1525/aa.1988.90.4.02a00030

Scott J, Kawahara A, Skevington J, Yen SH, Sami A, Smith M, Yack J (2010) The evolutionary origins of ritualized acoustic signals in caterpillars. Nat Commun 1:4. https://doi.org/10.1038/ncomms1002

Scott-Phillips TC, Blythe RA, Gardner A, West SA (2012) How do communication systems emerge? Proc R Soc Lond B 279:1943–1949. https://doi.org/10.1098/rspb.2011.2181

Searcy WA, Nowicki S (2005) The evolution of animal communication: reliability and deception in signaling systems. Princeton University Press, Princeton

Shettleworth SJ (2009) Cognition, evolution, and behavior. Oxford University Press, Oxford

Skyrms B (2010) Signals: evolution, learning, and information. Oxford University Press, Oxford

Sterelny K (2003) Thought in a hostile world: the evolution of human cognition. Blackwell, Oxford

Sterelny K (2007) Social intelligence, human intelligence and niche construction. Phil Trans R Soc B 362:719–730. https://doi.org/10.1098/rstb.2006.2006

Sterling P, Laughlin S (2015) Principles of neural design. MIT Press, Cambridge, MA

Stevens M (2013) Sensory ecology, behaviour, and evolution. Oxford University Press, Oxford

Taylor PD (1992) Altruism in viscous populations — an inclusive fitness model. Evol Ecol 6:352–356. https://doi.org/10.1007/BF02270971

Taylor PD, Frank SA (1996) How to make a kin selection model. J Theor Biol 180:27–37. https://doi.org/10.1006/jtbi.1996.0075

Templeton JJ, Kamil AC, Balda RP (1999) Sociality and social learning in two species of corvids: the pinyon jay (*Gymnorhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*). J Comp Psychol 113:450–455. https://doi.org/10.1037/0735-7036.113.4.450

Thornton A (2008) Variation in contributions to teaching by meerkats. Proc R Soc Lond B 275:1745–1751. https://doi.org/10.1098/rspb.2008.0268

Thornton A, Clutton-Brock T (2011) Social learning and the development of individual and group behaviour in mammal societies. Phil Trans R Soc B 366:978–987. https://doi.org/10.1098/rstb.2010.0312

Thornton A, McAuliffe K (2006) Teaching in wild meerkats. Science 313:227–229. https://doi.org/10.1126/science.1128727

Thornton A, Raihani NJ (2008) The evolution of teaching. Anim Behav 75:1823–1836. https://doi.org/10.1016/j.anbehav.2007.12.014

Thornton A, Raihani NJ (2010) Identifying teaching in wild animals. Learn Behav 38:297–309. https://doi.org/10.3758/LB.38.3.297

Thornton A, Samson J (2012) Innovative problem solving in wild meerkats. Anim Behav 83:1459–1468. https://doi.org/10.1016/j.anbehav.2012.03.018

Truskanov N, Prat Y (2018) Cultural transmission in an ever-changing world: trial-and-error copying may be more robust than precise imitation. Phil Trans R Soc B 373:20170050. https://doi.org/10.1098/rstb.2017.0050

Turner CR, Flynn E (2016) Learning by diffusion: Using diffusion experiments and social network analysis to understand the dynamics of cultural evolution. In: Obhi S, Cross E (eds) Shared representations: Sensorimotor foundations of social life. Cambridge University Press, New York, pp 503–524

Varela SAM, Teles MC, Oliveira RF (2020) The correlated evolution of social competence and social cognition. Funct Ecol 34:332–343. https://doi.org/10.1111/1365-2435.13416

Wagner RH, Danchin É (2010) A taxonomy of biological information. Oikos 119:203–209. https://doi.org/10.1111/j.1600-0706.2009.17315.x

West SA, Pen I, Griffin AS (2002) Cooperation and competition between relatives. Science 296:72–75. https://doi.org/10.1126/science.1065507

West SA, Griffin AS, Gardner A (2007) Evolutionary explanations for cooperation. Curr Biol 17:R661–R672. https://doi.org/10.1016/j.cub.2007.06.004

Whitehead H, Rendell L (2015) The cultural lives of whales and dolphins. University of Chicago Press, Chicago

Whiten A (2019) Cultural evolution in animals. Annu Rev Ecol Evol S 50:27–48. https://doi.org/10.1146/annurev-ecolsys-110218-025040

Whiten A, Byrne RW (1988) Tactical deception in primates. Behav Brain Sci 11:233–244. https://doi.org/10.1017/S0140525X00049682

Whitlock MC, Dyken JDV (2011) Altruism in viscous populations revisited: competition and altruism do not exactly cancel even in the island model. Evol Ecol Res 13:747–752

Wiley RH (2013) A receiver–signaler equilibrium in the evolution of communication in noise. Behaviour 150:957–993. https://doi.org/10.1163/1568539X-00003063

Wolf M, van Doorn GS, Weissing FJ (2011) On the coevolution of social responsiveness and behavioural consistency. Phil Trans R Soc B 278:440–448. https://doi.org/10.1098/rspb.2010.1051