

19 Social Learning and Teaching Overview

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Social learning has been defined as “learning that is facilitated by observation of, or interaction with, another individual (or its products)” (Heyes, 1994, p. 207), and has often been thought of as relatively cheap and less risky when compared to individual learning (Hoppitt & Laland, 2013). These advantages make social learning an adaptive way to gain information about the environment, which may explain why it is taxonomically widespread, being found in mammals, birds, and insects, and across a variety of behavioral domains including skills, calls, predation, mates, and resources (Hoppitt & Laland, 2013).

The term “processes” is used in the social-learning literature to describe what information an individual attends to and processes when learning from others. Several authors have classified social-learning processes (e.g., Galef, 1988; Whiten & Ham, 1992; Heyes, 1994; Hoppitt & Laland, 2013) and there are some differences between the classifications. However, there is a general consensus on the basic categorization of processes, which vary along a continuum from an inadvertent process, such as when an individual’s attention is merely drawn to a new resource by another individual “going about their business” and then learns for themselves (asocially), to active teaching of skills by experienced individuals to naïve ones. In some instances, this information transmission is sufficient to propagate the diffusion of novel behavior patterns through animal populations, and to maintain distinct behavioral traditions between different populations of the same species. These traditions are regarded as analogous to human culture in many respects and have been described as “culture.” However, the use of this term indicates little more than that the behavior concerned has been learned socially, and does not necessarily imply that the animals concerned are unusually intelligent, or that they have exceptional linguistic or cognitive capabilities. Indeed, key aspects of human culture – biases in information transmission, cumulative culture, and teaching – and whether nonhumans display evidence of them are major topics of research in the field of animal social learning.

Social Learning in Animals

Underlying culture in nonhuman animals is a capacity for “social learning.” Although social learning, as an umbrella term, may include active teaching (see Hoppitt et al., 2008) or explicit communication, researchers of nonhumans mean no more by the term than the acquisition of information from others who inadvertently emit it. Social learning is frequently contrasted with individual or asocial learning, trial-and-error learning and innovation, in which animals learn exclusively on the basis of their own personal experience, without recourse to social cues or guidance. In any instantiation of social learning, the learner or receiver of information is generally described as the “observer,” while the transmitter of information is called the “demonstrator.” Social learning occurs when the transmission of information between two animals results in the observer learning from the demonstrator. Frequently, the observer learns through social interaction to perform the same behavior as that exhibited by the demonstrator and, if repeated among other animals, this process can result in the spread of a particular behavior pattern and behavioral homogeneity in a population. Less frequently, animals may learn by observation to perform a different behavior from that exhibited by the demonstrator.

Social learning among animals has been of interest to scientists from a number of different disciplines. Psychologists have traditionally been interested in animal learning. Contemporary animal learning theory describes learning in animals according to three types of experience that cause a change in behavior: a single stimulus (Stimulus (S) learning, e.g., habituation or sensitization); an association between two external stimuli (Stimulus–Stimulus (S–S), or classical conditioning), or to an association between an external stimulus and an animal’s behavioral response (Stimulus–Response (S–R), or Response–Reinforcer (R–R) learning, or operant/instrumental conditioning). Arguments abound as to whether there is anything different or special about social, compared with asocial, learning, and whether social learning can be adequately explained in conditioning terms (see Kendal et al., 2018).

Recent evidence may be taken to indicate that social and asocial learning depend upon the same learning mechanisms (reviewed by Heyes, 2011), rather than the alternative, that social learning is dependent upon a set of special-purpose modules evolved many times in different taxonomic groups as adaptive specializations for group living. This evidence includes findings that social learning and asocial learning covary. In birds and primates, social and asocial learning abilities are correlated positively across species even when accounting for differences in body mass, brain volume, phylogeny, and research effort (see Street, Navarrete, Reader, & Laland, 2017). Social learning abilities have also been found in solitary species, the common octopus and red-footed tortoise, which might not be expected if social learning evolved independently of

asocial learning, and in response to the selection pressures of social living. However, solitary species do, in fact, occasionally interact with conspecifics or heterospecifics, thus social learning remains useful to them (Kendal et al., 2018). Finally, social learning has the same key features across diverse species, including humans. That is, across species, the main types of social learning occur under the same observable conditions as the three main types distinguished for asocial learning. Thus, social and asocial learning may be seen to depend upon the same learning mechanisms, which are taxonomically general rather than specialized. Indeed, Heyes (2011) recently claimed that, at the cognitive level, all that is “social about social learning” is the biasing or tuning of input mechanisms (perception, attention, and motivation) toward other agents, as the actual long-term encoding of information is mediated by general learning mechanisms. However, see Kendal et al. (2018) for a more in-depth discussion of the biological basis of social learning that posits several lines of evidence contrary to this opinion.

Social learning has also been of interest to ethologists and behavioral ecologists because it seems to allow animals to learn about their environments rapidly and efficiently, without having to engage in potentially costly or hazardous learning trials, or expend considerable time and energy exploring the environment. Animals can learn which foods to eat, acquire food processing skills, learn to identify predators, learn which members of the opposite sex to mate with, or develop songs and calls, by exploiting the knowledge base of more experienced conspecifics (Heyes & Galef, 1996). Social learning can be regarded as a short cut to learning about the environment, but may incur a cost if the acquired knowledge is inappropriate or outdated. Finally, evolutionary biologists, biological anthropologists, and archaeologists also study animal social learning, because it is accorded a prominent role in the evolution of human culture.

Although definitions of human culture vary, one central feature is the transmission of acquired information between individuals through social-learning processes. Many researchers believe that an understanding of the ways in which social learning operates in animal populations will generate insights into the evolutionary roots of human culture. Social learning is regarded as pivotal to a number of social-intelligence hypotheses that maintain that the evolution of high intelligence or large brains was driven by a capacity for social learning and culture (Byrne & Whiten, 1988; Whiten & van Schaik, 2007). Linked to such theories is the suggestion by many psychologists that more complex forms of social learning might be indicative of the animal concerned possessing unusual or sophisticated psychological capabilities (Heyes, 1994). For instance, it has been suggested that for an animal to accurately imitate the motor patterns of another animal it must be conscious, capable of taking the other animal's perspective, unusually intelligent, or capable of intentional action. Although such claims are now hotly disputed, social learning is inextricably linked to other factors believed pivotal in the

evolution of humanity's socio-cognitive niche (Whiten & Erdal, 2012). Indeed, a current controversy in this area centers on explanations of human evolution that variously highlight our cognitive (Pinker, 2010) or cultural (Boyd, Richerson, & Henrich, 2011) capacities as crucial. Key to the latter is the potential role of imitation and teaching in promoting the high-fidelity transmission deemed necessary for cumulative culture – the ability to generate complex cultural traits by building upon existing behavior patterns, generation after generation – widely thought to enable the extraordinary achievements of humans (Boyd & Richerson, 1985; Galef, 1992; Tomasello, 1994). Accordingly, a major unanswered question in the animal social-learning field is why nonhumans do not have, or have impoverished forms of, cumulative culture (Dean et al., 2014).

Early Studies of Animal Social Learning

The study of social learning in animals dates back to Darwin, and flourished as a result of attempts to demonstrate mental continuity between humans and animals in order to prove that humans had evolved. For many Victorian scientists, demonstrations of social (then termed “imitative”) learning in animals was seen as providing evidence of an evolutionary origin of the higher mental faculties of humans. Imitation was regarded as intermediate in psychological complexity between animal instinct and human reasoning (Boakes, 1984). The verb “to ape” and the phrase “monkey see monkey do” are manifestations of the then commonly held view that primates are frequent imitators of each other's behavior.

While numerous observations of imitative behavior in primates and other animals were reported in the late nineteenth century, attempts to demonstrate imitation proved problematic. Likewise, the study of teaching in animals was hampered by an anthropocentric stance that defined teaching according to the intention of the tutor to educate, something that is difficult to infer in nonhumans. It became apparent that there are many processes that can result in two animals expressing similar behavior. Researchers began to realize that anecdotal stories concerning animals in uncontrolled environments would not provide satisfactory evidence to address this issue. In the first decades of the twentieth century, Edward Thorndike attempted to introduce some scientific rigor into investigations by carrying out controlled experiments exploring what he called imitation in cats, dogs, and monkeys (Galef, 1988). Thorndike's experiments led him to the controversial conclusion that there was no evidence that animals could “from an act witnessed learn to do an act.” Out of the controversy there emerged two distinct research traditions in the study of social learning: a laboratory experimental tradition, dominated by experimental psychology; and a second tradition that carried out observations of natural populations of animals, dominated by ethologists and primatologists. The laboratory approach has focused on investigating the psychological

mechanisms underlying social learning. In contrast, field studies have reported behavior patterns spreading through animal populations, or cultural traditions. One of the earliest studies of social learning in wild animals was carried out in a population of Japanese macaques, where a young female *Imo* began washing sweet potatoes provisioned on a beach before eating them. This previously unobserved behavior was subsequently seen to increase in frequency in the troop, with most of the troop eventually adopting the potato-washing behavior, presumably by learning from each other (Kawai, 1965). More recently, researchers have developed experimental approaches to study the spread of learned information through animal populations, including transmission chain and diffusion studies (reviewed in Whiten & Mesoudi, 2008). In addition, mathematical approaches have explored the conditions under which social learning is expected to evolve, and the evolutionary consequences of social learning. Finally, the field has recently seen a marrying of experimental and ethological approaches in the development of statistical methods, enabling robust investigation of social learning in wild animals (reviewed in Kendal, Galef, & van Schaik, 2010a). We now turn to an overview of animal social learning in captivity and in the wild.

Animal Social Learning in Captivity

Social Learning Processes?

Modern laboratory experiments investigating social learning in animals commonly train animals (called demonstrators) to perform a target behavior (e.g., to push a lever to get a food reward), pair these demonstrators with untrained experimental subjects (called observers) that watch the demonstrator perform the behavior, and then test the observers alone to establish whether they have learned to perform the target behavior (Galef, 1988). Frequently, the rate at which the subjects learn to perform the behavior is compared with control subjects that have received different forms of observational experience. Such experiments have established that there are a number of ways that animals can learn socially, the variants reflecting the nature of the observer's learning and the type of information transmitted from demonstrator to observer. For instance, in the lever-pressing example, the observers might learn at an accelerated rate relative to controls: (a) because they learned of the presence or significance of the lever; (b) because they learned of the presence of food; (c) because their observational experience allowed them to form an association between the depressed lever and the appearance of food; or (d) because they formed an association between the action of pressing the lever and the appearance of food. In addition, there are other nonsocial-learning processes that could result in an elevation in the observers' performance, for example, if observation changes the observer's motivational state.

Such experiments have resulted in a multitude of terms to describe the different processes that can result in social learning, and spawned a host of classificatory schemes. At present, there is only partial consensus over the terminology. One reason for the lack of progress in consensus is that early classifications stemmed from the goal of providing a list of mechanisms to be ruled out by researchers if they are to claim “true” imitation (that is, matching of specific motor patterns between observer and demonstrator). Thus, until recently, relatively little attention was paid to distinguishing among the many potential nonimitative processes. In addition, some terms are defined using criteria that are not directly observable (i.e., processes inside individuals, such as “goals” or “intentionality”) or that are not amenable to experimental manipulation in the laboratory.

In the most recent classification scheme by Hoppitt and Laland (2008) nine social-learning processes are identified. The simplest forms of social learning do not affect the form of a learned behavior, influencing only when animals perform the behavior. Here, *social facilitation* occurs when a conspecific’s presence increases the likelihood that an individual performs an action (e.g., bird song, Jesse & Riebel, 2012) whether or not the conspecific is performing that action (Hoppitt & Laland, 2013). Similarly, *response facilitation* occurs when the presence of a conspecific performing a particular behavior (e.g., placing a blade of grass in the ear in chimpanzees, van Leeuwen, Cronin, & Haun, 2014) triggers its performance in another already possessing the behavior in their repertoire (Byrne, 1994).

Animals may also learn the exact form of a behavior for themselves (asocially), after having their attention drawn to a particular location (*local enhancement*, Spence, 1937) or stimulus (*stimulus enhancement*, Thorpe, 1956) by the behavior of another animal. Thus, observation of another individual exposes the observer to a single stimulus (S learning) leading to a change in the observer’s behavior. For instance, it was established that wild British birds learned to peck open milk bottle to drink the cream (Hinde and Fisher, 1951) due to having their attention drawn to milk bottles by the by-products (open tops) of feeding birds’ behavior (Sherry & Galef, 1990). Likewise, due to a tendency to shoal, knowledgeable guppies may lead naïve individuals to a novel food source location (Laland & Williams, 1997). “Observational conditioning” occurs when the observer learns to what circumstances a behavior should be a response. Thus, another individual’s behavior increases the probability that the observer will be exposed to a relationship between two external stimuli (S–S learning), leading to a change in the observer’s behavior. For example, infant rhesus monkeys learned to respond to the presence of a snake with fear and avoidance behavior through observations of the screams and avoidance behavior of adults when exposed to snakes (Mineka & Cook, 1988).

Observational learning occurs when the observer learns of a relationship between a behavior and its outcome (response–reinforcer R–S learning). Thus, another individual’s behavior facilitates stimulus–response (S–R) learning,

resulting in a change in the observer's subsequent behavior. Within this class of social-learning processes is "*imitation*," which is said to occur when the observer learns from the demonstrator to perform a specific motor pattern in a particular context or as when "B learns from A some part of the form of a behavior" (Whiten & Ham, 1992, p. 247). Individuals do not learn actions by trial-and-error (asocial) learning but by recreating them through observing those performed by another. The two-action method has been widely deployed to test for imitative ability (Dawson & Foss, 1965) and has typically involved a puzzle box that can be solved using either of two (or more) alternative solutions. If observers copy the action that they have seen performed, rather than the other actions that are possible and equally rewarding, it is argued that this provides evidence of imitation. Whiten et al. (2005) devised such a puzzle box (the "*panpipes*"), which could be solved using a "lift" or "poke" method to gain a food reward. A single chimpanzee from each of two groups was trained to use one of the two methods before being reintroduced to their group. Having seeded the group with a particular method to solve the puzzle box, Whiten, Horner, and de Waal (2005) observed that naïve individuals within the group were more likely to adopt the method they had witnessed than the alternative. A later study, where no demonstrator is present and the key feature of the task is moved as if by a ghost, confirmed that such learning involved more than observation of the affordances of the puzzle box (Hopper, Lambeth, Schapiro, & Whiten, 2015).

Imitation has proven to be the most elusive and contentious of all of the social-learning processes (Hoppitt & Laland, 2013) with researchers calling for additional criteria to the definition. Thus, we have seen further delineations to deal with, for example, the problem of attributing imitation when a behavioral motor pattern is not novel to the observer. *Contextual imitation* specifies that an individual learns to use an action already in its repertoire in a new context by observing another and *production imitation* specifies that the observer learns novel actions, not previously in its repertoire, from observing another (Byrne, 2002). In addition, production imitation allows for imitation of novel behavioral sequences comprising behaviors that exist in the behavioral repertoire. Finally, whether imitation demonstrates intentionality and insight (Tomasello, 1996) such that individuals infer the goals (Tomasello, Carpenter, Call, Behne, & Moll, 2005) of the demonstrator has been debated (Heyes, 1994; Byrne, 1999). Accordingly, *rational imitation* refers to observers making a rational choice about how much of the demonstrator's behavior is relevant to copy (Gergely, Bekkering, & Kiraly, 2002). For example, there is evidence that in chimpanzees (Buttleman, et al., 2007) and dogs (Range, Virany, & Huber, 2007) individuals are more likely to copy an unusual behavior (e.g., in dogs using the paw to pull a wooden rod) for achieving a goal if there is no obvious reason for its use by the demonstrator than if there is (e.g., inability to use the mouth, as biting a ball). Here, the unusual or inefficient behavior of the demonstrator can be assumed not to be

“intentional” and the observer will copy it with low fidelity and use a more usual/efficient means of achieving the same goal.

Where individuals copy the results of a demonstrator’s behavior rather than the actions themselves, this may be called *emulation* (Custance, Whiten, & Fredman, 1999; Byrne, 2002), which subsumes several processes (Hoppitt & Laland, 2008). In the previous example, the dog who used its mouth to pull a wooden rod to receive a reward despite the demonstrator using its paw to do so, could be said to have used *goal emulation* to copy the goal, or achieve the same result, through their own trial-and-error learning (Whiten & Ham, 1992). A further example is that of chimpanzees, who parse out causally irrelevant actions in their copying of novel behavior patterns (Horner & Whiten, 2005). This definition is problematic, in that it refers to the unobservable observer’s understanding of the demonstration but is operationalized in terms of their observable behavior. It is recognized that there are many ways in which the results of a demonstrator’s behavior may be replicated including *object movement reenactment*, whereby observers recreate the movements of the objects manipulated by the demonstrator. For example, pigeons, chimpanzees, and children are able to solve a simple task when observing objects that move as if by a ghost (e.g., using fishing line), with no demonstrator visible (Hopper, 2010). Such “ghost controls” are often used to distinguish between imitation and emulation. Finally, *affordance learning*, whereby observers learn what can be done with an object, is variously defined as emulation (Hopper, 2010) or observational conditioning (Hoppitt & Laland, 2008).

Although many researchers of animal social learning implicitly use the term to mean inadvertent social learning, *teaching*, or the active facilitation of learning in others, can be viewed as a social learning process in parallel to the classification of inadvertent social learning given above (see Hoppitt, Brown et al., 2008).

The study of animal teaching took off when Caro and Hauser (1992) defined teaching from a functional perspective according to observable criteria and has become a lively area of debate since. Teaching is currently recognized as when an individual (the tutor) modifies its behavior only in the presence of a naïve observer (the pupil) at some cost or without immediate benefit to itself, resulting in the pupil acquiring knowledge or skills they otherwise would not, or more rapidly/efficiently. This is not to say, however, that pupils and tutors cannot both reap fitness benefits from the cooperative endeavor (Thornton & Raihani, 2015). Following a taxonomic review of evidence for teaching in animals according to this definition, Hoppitt, Brown et al. (2008) proposed a caveat in order to guard against false report of animal teaching by ruling out behavior that might be adapted for a function other than transmitting knowledge or skills to others. Thus, where behavior may increase the inclusive fitness of a tutor (e.g., parental provisioning of offspring) regardless of whether knowledge is transmitted to the pupil (e.g., dietary preferences), evidence is required that the tutor’s behavior has been modified by selection

to promote learning in the pupil. An example of such evidence would be if tutors evolved the means to respond to feedback from the pupil such that they provide learning opportunities contingent on the pupil's knowledge/skill state. Note that while anthropocentrically we may interpret this as inferring metacognition on the part of the tutor, this is not necessary in either humans or nonhumans (see Kendal et al., 2018). Moreover, a restriction of teaching to the “passing on of skills, concepts, rules and strategies” rather than “telling” another of a fact such as a resource location (Leadbeater et al., 2006; Csibra, 2007) would impose stricter criteria on nonhuman teaching than human teaching (much of which would be classed as “telling”).

Laboratory investigations of teaching in tandem running ants have become a gold standard in the field of captive-animal social learning. Here successful foragers guide nest-mates to newly discovered nest sites or food resources. There is a *cost* to the tutor, as they take four times as long to reach food, and a *benefit* to the pupil, in that they find food significantly faster than when alone (Franks & Richardson, 2006). Moreover, it is more efficient for knowledgeable individuals to carry naïve ants directly to food or new nest sites, yet doing so hinders learning (Leadbeater & Chittka, 2007). Although the behavior increases the tutor's inclusive fitness as the nest-mate may help carry food back to the nest or individuals to the new nest site, there is evidence that the behavior is adapted to the function of teaching. First, tutors respond to feedback in that they only run rapidly when receiving a tap from the antennae of pupils, enabling them to remain in close contact (Franks & Richardson, 2006). In addition, when learning of pupils is experimentally inhibited by reducing their vision and ability to take in route landmarks, tutors evaluate the progress of their pupils and adjust their running appropriately (Franklin, Richardson, Sendova-Franks, & Franks, 2011).

Culture?

Having established the variety of ways in which animals may learn socially, we consider the implications of social learning for animals. The question of whether nonhuman animals exhibit culture, and the importance of this for understanding human behavior, depends fundamentally on definitions of culture. Definitions range from those that deem a species cultural if it exhibits traditions transmitted via some form of social learning (Laland & Janik, 2006) or displays a repertoire of more than one tradition (Whiten & van Schaik, 2007) to those requiring that transmission involve teaching, imitation, or the generation of group-specific norms and ethnic markers (Tylor, 1871). One point of consensus, however, is the necessity, if not sufficiency, of social learning in underpinning culture.

Attempts to investigate animal cultural traditions experimentally have moved away from the demonstrator–observer dyadic approach toward group-level studies under controlled conditions in captivity. Specifically, these

studies have attempted to provide direct evidence of the involvement of social learning in the group-level behavioral patterning, reminiscent of human cultures, seen in many wild animals. These studies have included “diffusion chains” and “open diffusions.” In diffusion chains, subject 1 observes a model performing action A or action B, before they become the model for subject 2 in the chain, and so forth. As the founder population of trained demonstrators is gradually replaced by untrained animals (replacements representing the turnover of pseudo-generations), researchers explore whether the target behavior persists in the population (e.g., guppies: Laland, Richerson, & Boyd, 1993). In open diffusion, a trained model demonstrates action A or B to a group of naïve subjects and the increase in the number of individuals displaying the target behavior over time is recorded (e.g., pigeons: Lefebvre & Palameta, 1988). For example, diffusion-chain studies of captive chimpanzees, involving the use of novel extractive foraging tasks/puzzle boxes (or “artificial fruits” such as the panpipes discussed earlier), have shown they can sustain foraging traditions, across pseudo-generations through high-fidelity social learning (Horner, Whiten, Flynn, & de Waal, 2006). Moreover, over past decades captive groups have come to be distinguished by different cultural repertoires of experimentally induced traditions, and transmission between groups (through shared windows) has been documented (see Whiten et al., 2007). Taken together, such evidence implies that the behavioral variation observed in wild chimpanzees (Whiten et al., 1999) is cultural.

Studies of captive animals have also proven enlightening regarding the question of cumulative culture (see Miton & Charbonneau (2018) for a summary). The precise definition of cumulative culture is currently hotly debated (Mesoudi & Thornton, 2018). However, in general researchers assume that cumulative culture variously involves: (1) evidence of the social transmission of the trait/behavior; (2) evidence for trait modification over time (repeated episodes) such that it is improved in terms of efficiency and/or complexity; (3) evidence of an enhanced level of complexity (or efficiency), a useful yard stick being that it exceeds what a single individual could reasonably invent alone (Tennie, Call, & Tomasello, 2009; Dean, Vale, Laland, Flynn, & Kendal, 2014). Again, there have been studies of captive primates using extractive foraging tasks in this context. Many have found no evidence that primates are able to improve upon a behavior that they have observed others perform, even when the behavior in question is not beyond what an individual can discover for themselves (e.g., chimpanzees: Marshall-Pescini & Whiten, 2008; Dean et al., 2012; capuchins: Dean et al., 2012). There is, however, evidence that animals can be coaxed into displaying cumulative problem solving by making previous less efficient/complex methods unavailable (chimpanzees: Davis, Vale, Schapiro, Lambeth, & Whiten, 2017; Vale, Davis, Lambeth, Schapiro, & Whiten, 2017; orangutans: Lehner, Burkhardt, & van Schaik, 2011). Alternative studies using transmission chains of different types of tasks have also been revealing. Baboons have been found capable of

improving the efficiency of a behavioral trait across pseudo-generations (Cladière, Smith, Kirby, & Fagot, 2014). However, the extent to which this represents cumulative culture has been questioned as the task involved copying a pattern with greater accuracy (akin to language evolution) rather than in order to improve reward received. A study of pigeons cumulatively improving the efficiency of homing routes is compelling (Sasaki & Biro, 2016) as is a study demonstrating cumulative improvement of naïve zebra finch song toward the wildtype (Feher, Wang, Saar, & Tchernichovski, 2009) though each has received critique.

Across the many studies of animal social learning, it became apparent that different aspects of social interaction impede, or propitiate, the diffusion of information. The structure of animal populations (dominance relations, familiarity of individuals, spatial positioning, sex, age, and size differences) strongly influences the pathways by which learned information spreads, a phenomenon known as “directed social learning” (Coussi-Korbel & Fragasy, 1995). For instance, novel skills often spread at different rates among juveniles and adults, among the two sexes, or within and between family groups. Where this differential information flow is for learning purposes, rather than a by-product of directed social learning, we can infer social learning strategies (Laland, 2004) or transmission biases (Boyd & Richerson, 1985). These strategies or biases influence whether or not individuals use social learning and, if they do, from whom they learn. This has become a lively area of research that we now review.

Social Learning Strategies/Transmission Biases?

Theoretical analyses have explored the circumstances under which natural selection will favor reliance on social learning, as opposed to asocial learning or evolved non-learned behavior (see Laland et al., 1996, for an overview of this literature). A consensus has been reached that the issue hangs, in part, on patterns of variability in the environment. In an environment that is changing comparatively slowly, or that exhibits relatively little spatial heterogeneity in resources, populations are able to evolve appropriate behavior patterns through natural selection, and learning is of little adaptive value. In contrast, in rapidly changing or highly variable environments, asocial learning pays. Here, natural selection cannot track environmental fluctuations quickly enough, while social learning is unreliable because it may lead individuals to acquire outdated or locally inappropriate behaviors. It is intermediate rates of change and patterns of spatial heterogeneity that favor social learning, and within this window vertical transmission of information (social learning by offspring from parents) is thought to be an adaptation to slower rates of change than horizontal transmission (social learning among unrelated individuals of the same cohort).

Although these findings are theoretically robust, it is only recently that they have begun to be validated with empirical studies of animals (reviewed in

Kendal et al., 2005, 2009a, 2018; Rendell et al., 2011). For instance, we did not know whether contemporary populations of animals capable of social learning actually do switch between social and asocial learning depending on the pattern of environmental variability they experience in pertinent resources. Providing a partial answer to this question is a study of wild caught sticklebacks, where the fish ignored social information provided by other foraging conspecifics when their personal foraging information was highly reliable (representing a non-variable environment), but were more likely to copy others as their own information became outdated and thus potentially unreliable (van Bergen, Coolen, & Laland, 2004).

More generally, attention has recently turned to what other factors affect reliance on social learning. In the most recent collation of such studies (Kendal et al., 2018), there is evidence that individuals copy others when asocial learning would be costly. For example, bees (Baracchi et al., 2017), fish (Laland et al., 2011), and monkeys (Kendal et al., 2009b) use social information more when a task is difficult as this increases energetic or time costs of acquiring the solution asocially. Animals are also more likely to use social information when they are uncertain as they have no relevant information (e.g. fish: Kendal et al., 2004, chimpanzees: Kendal et al., 2015, ants: Stroeymert et al., 2017) or their prior information is unreliable or outdated (van Bergen et al., 2004). There is also evidence of other state-based biases whereby the use of social information is influenced by the state of the learner. For example, low- and mid-ranking captive chimpanzees have been found more likely to use social information than high ranking ones (Kendal et al., 2015), gravid female fish are more likely to use social information than non-gravid ones (Webster & Laland, 2011), and bats (Jones et al., 2013) and bumblebees (Jones et al., 2015) copy others more when dissatisfied with the payoff of their current behavior.

Animals may also be biased toward copying individuals based on their characteristics regardless of whether the to-be-copied trait is influential in that characteristic. For example, in some instances chimpanzees preferentially observe and copy dominant individuals (Horner et al., 2010; Kendal et al., 2015) and sticklebacks preferentially copy larger (often older) over smaller fish (Duffy, Pike, & Laland, 2009). These strategies are heuristics thought to lead to the copying of generally successful individuals that therefore ought to display behavioral traits worth adopting. Although the evidence for frequency-dependent biases in social learning is equivocal, chimpanzees copy what the majority of individuals they have observed do rather than the minority (Haun et al., 2012). Finally, there is evidence that sticklebacks (Kendal et al., 2009c) and chimpanzees (van Leeuwen, Cronin, Schütte, Call, & Haun, 2013; Vale et al., 2017; van Leeuwen & Call, 2017) exhibit content dependent biases such that they may use social learning if the payoff of a demonstrator's behavior is better than their own. Overall, the current evidence indicates that these social learning strategies are used flexibly by

individuals depending upon context, developmental experience, or individual differences and that multiple strategies may act in concert as biases of individual's learning (Kendal et al., 2018).

Biological Basis of Social Learning?

The plethora of competing terms for social learning processes and social learning strategies and their diverse use reflect our poor understanding of the genetic, neural, or physiological processes that underlie the processing of sensory information, the associationist or transformational organization of this information, and the production of motor patterns, during social learning. Our knowledge is, however, increasing in this area. Social neuroscientists highlight a “deep homology” in the mechanisms and structures of the “social brain” across diverse taxa (Tremblay et al., 2017), while studies of primates have emphasized how their brains, particularly with respect to encephalization and the neural basis of imitation, are organized for “socio-cultural” processing (Whiten & van de Waal, 2016). For example, the neural correlates of vocal imitation in song birds have been known for many years and, with the discovery of “mirror neurons” in macaque monkeys (Rizzolati & Craighero, 2004), the neural mechanisms of motor imitation have been deduced. These neurons are found in the ventral premotor cortex (area F5) and in the inferior parietal lobule (area PF). Both of these brain areas are interconnected and also connect with the superior temporal sulcus (STS), which contains visual neurons that respond to seeing the actions of others. The mirror neurons are active when monkeys perform goal-directed actions themselves and when they observe someone else performing such an action. This circuitry, which enables the coding and mapping of observed actions onto the motor repertoire of the observer, would seem important in facilitating imitation. Indeed, in humans areas 44 and 45 of the left inferior frontal gyrus (IFG), a region subsumed by Broca's area and the homologue of monkey F5, are specialized for imitation according to functional magnetic resonance imaging (fMRI) studies. As further detailed by Iacoboni (2005), mirror neurons in monkeys code the likely future actions of others, enabling the anticipation of other's intentions, and change their activation responses according to observational experience, potentially enabling the learning of novel actions as required in imitation.

More recent neuroscientific data also point to dedicated mechanisms for social learning. For example, neurophysiology, neuroimaging, and lesion studies, in animals all indicate a specialization in the anterior cingulate cortex lying in the gyrus (ACCg) for processing social information (Apps et al., 2016). This region shows neuronal activity akin to trial-and-error learning but only when monitoring the behavior of others. Other medial prefrontal cortex (mPFC) subregions mostly signal in an egocentric frame or in both egocentric and allocentric frames. Thus these regions may contribute to integrating information regarding one's own actions and those of others to

update behavior (Apps & Sallet, 2017), potentially underlying payoff-biased social learning strategies (Kendal et al., 2018). Thus, these findings weaken the argument (Heyes, 2011) that social learning relies only on the neural mechanisms underlying asocial learning.

Experimental approaches with captive animals have greatly enhanced understanding of social learning in nonhumans, and developed the methodologies and conceptual tools to further our understanding. However, they do not tell us directly whether social learning can be implicated in the natural behavioral variation seen in animals in support of claims for animal culture. Accordingly, we now turn to the increasing evidence of social learning in wild animals.

Animal Social Learning in the Wild

Without an understanding of social learning in the context in which it evolved, we cannot hope to elucidate the interaction between biological and cultural evolution (Kendal et al., 2010a). However, in the field it is difficult to establish reliably whether or not a behavior genuinely is socially learned (as opposed to learned independently by each animal), to determine whether local traditions reflect different cultural repertoires or varying ecological resources, or to investigate the biological and social processes underlying the diffusion of information (see Laland, Kendal, & Kendal, 2009).

Social Learning Processes?

There are a huge number of reports of the spread of novel behavior patterns in populations of wild animals. Well-known examples include the transmission of dietary preferences by rats attending to cues on each other's breath, the learning of vocal dialects in song birds, and cetaceans, and tool-using traditions in primates and cetaceans (see Laland & Galef, 2009). However, hard evidence that putative animal traditions are socially learned has, until very recently, been limited. This led to researchers identifying social learning more directly in the wild using innovative experiments (reviewed in Reader & Biro, 2010), quantitative analyses (see Sargeant & Mann, 2009; Whitehead, 2009), and proxy measures of social learning, such as patterns of affiliation and observation. For instance, in both wild capuchin monkeys and chimpanzees evidence was reported that individuals selectively watch others from whom they can learn skills they have yet to master (Biro, Inoue-Nakamura, & Tonooka, 2003; Perry et al., 2003). It is always difficult to rule out the contribution of individual/asocial learning and practice in such studies, however.

Statistical methods for assessing the likelihood of asocial learning being responsible for an observed pattern of behavior, permitting inference of social

learning when asocial learning has been deemed improbable, have also been developed (reviewed in Kendal et al., 2010a). Likewise, mathematical models can be fitted to phylogenetic data to tease apart the role of genetics and culture in population level behavioral variation (Lycett, 2010). These methods have been applied to wild lemurs, capuchin monkeys, chimpanzees, cetaceans, song birds, meerkats, and other species. Perhaps the most persuasive of these studies are those that document naturally occurring novel behavioral traditions rather than experimenter-induced ones. Two such studies use a method known as network-based diffusion analysis (NBDA), which infers social learning (in addition to asocial learning) if the pattern of spread of information through a group is related to the social relationships between individuals. In humpback whales, the spread of a sophisticated lobtail feeding behavior, over twenty-seven years, has been reported as due to social learning (Allen, Weinrich, Hoppitt, & Rendell, 2013), and in chimpanzees the spread of a newly observed moss-sponging behavior in the Sonso community (Budongo forest, Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014), was better predicted by social learning than repeated asocial learning. The researchers were even able to calculate the strength of social learning, finding that individuals were 14.9 times more likely to learn moss-sponging following each observation of the behavior.

Although the field has come far in recent years in being able to identify social learning in the wild, elucidating the actual social-learning processes involved is limited due to the lack of control over variables in these contexts. However, a few studies have managed to identify the underlying processes. In an early attempt (Kendal et al., 2007) quantified and modeled the extent to which social learning influenced the rate of approach and subsequent solving of a novel task in groups of freely interacting (captive) callitrichid monkeys, finding evidence for stimulus enhancement but not observational learning. Using a different approach, wild banded mongooses have been shown to exhibit contextual imitation in the transmission of extractive foraging techniques, akin to biting or smashing bird eggs, between adults and pups (Muller & Cant, 2010). Moreover, in wild meerkats, Hoppitt, Samson, Laland, and Thornton (2012) used analytically extracted statistical patterns in individuals' social interactions to identify no less than nine different learning processes underlying foraging behavior, including local enhancement, emulation, and a process they termed "observational perseverance." One conclusion from the latter study was that maintenance of behavioral traditions need not require imitation or teaching but social-learning processes that are option-specific and prevent generalization to other solutions to the task at hand.

Finally, there are numerous studies of wild animals indicating active social learning or teaching. There is suggestive evidence for teaching in wild felids, cetaceans, primates, raptors, and bees (see Hoppitt et al., 2008). As yet, there are also two species with strong quantitative evidence that meets the aforementioned criteria for teaching. Wild meerkats teach pups how to handle

difficult prey such as scorpions and modify their behavior contingent upon the age of the pup (Thornton & McAuliffe, 2006); see also, in wild pied babblers (a group-living bird) adults actively condition nestlings to associate a specific *purr* call with food when they visit the nest (Raihani & Ridley, 2008). Production of this call is energetically costly for the tutor and, although it initiates begging in nestlings it does not increase the efficiency (which would be an immediate benefit to the tutor) of feeding visits for the tutor. This teaching, instead, pays off after fledging, when it is used to lead offspring away from danger or recruit them to food resources (Raihani & Ridley, 2007).

Culture?

Probably all vertebrates and many invertebrates will eventually be found to exhibit some form of social learning. These reports are often observations of acquired behavior patterns spreading through single populations. In other cases, distinct cultural variations may characterize the behavioral repertoires of different populations of the same species. For instance, much birdsong is thought to be learned from older males, and frequently regional song dialects characterize neighboring populations. In 1999, an ambitious large-scale study collated data from seven field sites to reveal thirty-nine chimpanzee behaviors that were shared by at least several members of a population but were absent in others (Whiten et al., 1999). For instance, ant-dipping (using a stalk to fish for ants) is reported in some but not all chimpanzee populations who have access to ants. These thirty-nine behaviors, not easily attributed to ecological or genetic factors, were deemed candidates for behavioral variations that were transmitted socially (i.e., cultural behaviors; but see Langergraber et al., 2010). Since this original work, diverse putative traditional behaviors have also been documented in capuchins (Panger et al., 2002; Perry et al., 2003), bonobos (Hohmann & Fruth, 2003), orangutans (van Schaik et al., 2003) and cetaceans (Rendell & Whitehead, 2001).

Although many researchers are skeptical in attributing culture to species based on the geographic, or ethnographic, method (Laland & Janik, 2006), independent evidence for social learning in the species, in captivity or the wild, strengthens the case. Moreover, recent studies have sought to identify whether neighboring groups display similar, or different, group-level behaviors. Migration of individuals between neighboring groups reduces genetic dissimilarity, and group proximity creates shared microenvironments, thus dissimilar behavior in neighboring groups can be more confidently attributed to social learning. For example, three neighboring chimpanzee groups in the Tai national park, Cote d'Ivoire, display different preferences in the tools they use to crack open *Coula* nuts, with two groups changing from stones to wood along with the increasing softness of the nut through the season, while the other group does not, despite the higher cost of collecting stones (Luncz, Mundry, & Boesch, 2012), sharing of migrants (Luncz & Boesch, 2014) and

meticulous verification of a lack of potential habitat variation (Luncz & Boesch, 2015). Likewise, in comparing the response of neighboring chimpanzee groups in Uganda, to a novel honey extraction task, Gruber, Muller, Strimling, Wrangham, and Zuberbühler (2009) found evidence of cultural differences in the evaluation of tool affordances. In accordance with some definitions of culture, these chimpanzees display community-specific cultures, one for using sticks and the other for using leaves as tools.

Field studies have also resulted in claims for cumulative culture in various species, including chimpanzees, Japanese macaques, capuchin monkeys, and New Caledonian crows (reviewed in Dean et al., 2014). Many of these claims are based on a presumption that variation across populations in the complexity of a putative behavioral tradition, represents different stages of cumulative evolution of that tradition. Take nut cracking as an example, which in its simplest form – and given a soft nutshell – may consist of hitting the shell onto a substrate with one's arm/hand. The use of wooden and stone hammers, evident in some chimpanzee populations, could therefore represent an elaboration of this percussive act (Boesch, 2003). The use of stone anvils, and the rare use of a stone to stabilize the anvil, observed in Bossou (Matsuzawa, 1994) would constitute further additional modifications to this percussive behavior (Boesch, 2003). While this account of progressive innovation is plausible, there is a lack of direct evidence showing that simple percussive acts must precede more elaborate ones. We do not know whether complex forms of nut cracking are beyond what can be invented by a single chimpanzee. Experimental evidence has shown that a chimpanzee was capable of *individually* learning more complex nut-cracking techniques that progressed from hitting one nut with another in session one, to hitting a nut on an anvil stone with a stone hammer by session six (Hirata, Morimura, & Houki, 2009). This suggests that complex tool combinations can occur by building on one's own discoveries (individual scaffolded learning) and may not require building on the developments of others (social learning coupled with innovation). Moreover, archaeological evidence from nut-cracking sites (Mercader et al., 2007) suggests that there has been little modification over the last 4,300 years. Similar critiques have been leveled at all claims of cumulative culture in wild animals. This is not to say, however, that with increased research investment we will not find sufficient evidence for some form of cumulative culture in wild animals.

Social Learning Strategies/Transmission Biases?

As many of the new methods to investigate social learning in the wild, take advantage of social network theory, they have facilitated investigation of directed social learning and/or transmission biases in the spread of information within and between populations. In a series of studies (Aplin et al., 2015; Aplin, Sheldon, & McElreath, 2017) evidence for conformity (but see van

Leeuwen et al., 2015, 2016) and against payoff-biased social learning in wild great tits has been reported. Conformist transmission has similarly been proposed (but see van Leeuwen et al., 2015, 2016) in wild female chimpanzees (Luncz, Wittig, & Boesch, 2015) and male vervet monkeys (van de Waal, Borgeaud, & Whiten, 2013) due to the apparent abandonment of an efficient foraging trait and adoption of its alternative upon migration to a new community displaying the alternative. When posing wild vervet monkeys with novel extractive foraging tasks evidence for a sex-biased social learning strategy was also found in that individuals learned more information from philopatric females (who potentially retain more ecologically relevant information) than from males that migrate to new territories (van de Waal et al., 2010). However, when the alpha male's behavior is of a higher payoff than the alpha female's, male, but not female, observers switch to copying the alpha male demonstrating a state-dependent and payoff-bias (Bono et al., 2018). Likewise, in wild capuchin monkeys and macaques, there is evidence for preferential attention to, and presumably learning, from older and more proficient tool users (Coelho et al., 2015; Tan, Hemelrijk, Malavijitnond, & Gumert, 2018). These findings confirm earlier captive work implying that multiple social learning strategies can coexist.

Influences of Animal Social Learning Research

As is evident from previous sections, animal social-learning research is a vibrant field and one which has influences in many tangential fields. As further examples, we now turn briefly to the role of social learning in our understanding of the evolution of intelligence and in animal conservation and welfare.

Evolution of Intelligence

Social learning has been central to a number of social-intelligence hypotheses suggesting that complex social behavior drove brain evolution and intelligence. Allan Wilson's (1985) concept of "behavioral-drive" explicitly emphasizes social learning, as he noted a positive relationship between relative brain size and rate of evolution in vertebrates. Big-brained species are said to exhibit greater behavioral plasticity, are more innovative, and are more capable of social learning than small-brained species. Thus, cultural traditions allow populations of animals to open up new niches and exploit novel resources, thereby exposing themselves to new selection pressures (known as "Niche Construction") (Odling-Smee, Laland, & Feldman, 2003; Sterelny, 2007), and accelerating the rate of fixation of mutations. Indeed, there can be no behavioral traditions or cultures without innovations at their inception. Thus, the field of animal social learning is closely tied to that of animal innovation.

Evidence in support of the behavioral-drive hypothesis includes a significant correlation between relative brain size and incidence of both innovation and social learning in primates (Reader & Laland, 2002) and birds (Nicolakakis, 2003) and intraspecific correlation of social and asocial learning in pigeons (Bouchard, Goodyer, & Lefebvre, 2007). Moreover, studies continue to uncover co-occurrence of enlarged brains, enhanced cognition, and sophisticated social-learning abilities in primates, cetaceans, and apes (Rendell & Whitehead, 2001; Emery & Clayton, 2004; Reader, Hagar, & Laland, 2011), with the most recent study suggesting these factors coevolved with sociality and extended lifespans in primates (Street et al., 2017). Likewise, the enhanced cognition of “enculturated” primates, raised by humans who emphasized socially guided exploration opportunities, may be taken as consistent with this hypothesis (see van Schaik & Burkart, 2011 for a review).

More recently, researchers have put forward the “Cultural Intelligence Hypothesis” as opposed to the “General Intelligence Hypothesis.” For Hermann, Call, Hernandez-Lloreda, Hare, and Tomasello (2007) – who gave a battery of tests to orangutans, chimpanzees, and 2.5-year-old children – this is evidenced in the fact that all species performed similarly in the domain of physical cognition but the children outstripped the other species when it came to social cognition. Thus, they propose that humans have a set of social-cognitive skills (theory of mind, social learning, communication), emerging early in ontogeny, for participating and exchanging knowledge in cultural groups. In a study of what underlies the apparently human unique capability of cumulative culture (the increase in complexity or efficiency of cultural artifacts across generations), Dean et al. (2012), when comparing capuchin monkeys, chimpanzees, and children, also isolated socio-cognitive factors including imitation, complex communication, and prosociality. Similarly, Whiten and van Schaik (2007) note a cross-species correlation of possession of complex culture (defined as a repertoire of multiple traditions) and social-intelligence supporting culture (e.g., imitation), namely in the great apes. They admit, however, the paradox of robust findings of imitation in birds yet little evidence for possession of cultural repertoires, and vice versa for monkeys. Recently, phylogenetic comparative analysis has corroborated arguments for a positive feedback process in the evolution of the human brain (Miller, Barton, & Nunn, 2019).

Animal Conservation and Welfare

The field of animal social learning has important implications for ethics, philosophy, and politics. Continuity of the human and the nonhuman animal mind affects ethical considerations in animal welfare and influences how we characterize humanity’s place in nature. Social learning may be used as a tool to enhance captive-animal welfare. For example, the social contagion of play may spread improved welfare in animal groups (Held & Spinka, 2011) and

contagion of affiliative behavior has been demonstrated in captive marmosets (Watson & Caldwell, 2010; Watson, Buchanan-Smith, & Caldwell, 2014).

Similarly, an understanding of animal social-learning processes and strategies can be used to enhance the conservation and management of species facing extinction due to anthropogenic changes and/or human-wildlife conflict (see Whitehead, 2010; Hockings et al., 2015; Greggor, Thornton, & Clayton, 2017). Finally, conservation priorities are influenced by an understanding of animal social learning, due to increasing awareness of the existence of not only genetic, but also cultural diversity, in animals, and how cultural change enables a flexible response to human disturbance (Gruber et al., 2019). Indeed, conservationists fight to preserve “culturally significant units” (for a review, see Whitehead, 2010) and the importance of culture is currently being considered in global treaties regarding the conservation of animals (e.g., Convention on the Conservation of Migratory Species of Wild Animals; Brakes et al., 2019).

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