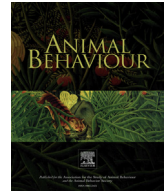




Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special Issue: Kin Selection

Psychological limits on animal innovation

Sarah F. Brosnan^{a,b,*}, Lydia M. Hopper^c^a Department of Psychology, Neuroscience Institute, Georgia State University, Atlanta, GA, U.S.A.^b Department of Philosophy, Georgia State University, Atlanta, GA, U.S.A.^c Lester E. Fisher Center for the Study & Conservation of Apes, Lincoln Park Zoo, Chicago, IL, U.S.A.

ARTICLE INFO

Article history:

Received 6 October 2013

Initial acceptance 3 January 2014

Final acceptance 18 February 2014

Available online 27 March 2014

MS. number: ASI-13-00834

Keywords:

conformity

conservatism

endowment effect

functional fixedness

innovation

invention

neophobia

social learning mechanism

transmission bias

Innovation is a way by which animals adopt a new behaviour or apply a current behaviour to a novel situation. Although exploring a new behaviour is itself risky for the animal, a growing body of research indicates that it is fairly widespread across animal species. While there have been explorations of when innovation is most likely and which individuals are most likely to innovate, less has been explored about the psychological mechanisms underlying innovation. Here we consider some psychological limits on innovation. We focus on five factors that may limit the invention of novel behaviours (neophobia, conservatism, conformity, functional fixedness and the endowment effect). The feature common to each of these is that individuals tend to stick with existing behaviours, or the existing uses of those behaviours, rather than exploring novel options. This in turn limits animals' willingness to try less common behaviours unless they are forced through circumstances to explore alternate strategies. Despite the similar functional outcomes, it is critical to understand the underlying mechanisms present in different situations in order to make strong predictions about when innovation is, or is not, expected to emerge. We then consider how transmission biases and social learning mechanisms influence and limit the spread of inventions among individuals. Of course, these 'limits' are beneficial in other circumstances, and throughout this review we consider the trade-offs for these psychological mechanisms.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Like many excellent scientists, Bill Hamilton was smart, creative, and loved what he did (Dawkins, 2000; Segerstråle, 2013). Additionally, he was noted for his willingness to think innovatively about problems in evolutionary biology, a risky proposition that led to 'glorious' results (Queller, 2001). As a result, while most scientists advance their field in incremental ways, Hamilton's innovations literally changed the foundations of evolutionary biology. If, however, the rewards to innovation are so great, why is it not more common in humans or other species?

While on the surface innovation seems to be an advantage, as it offers the opportunity for individuals to be more productive, exploit novel resources, or adapt to changing environments, there are also limits to the benefits (Reader & Laland, 2003). After all, the current solution has allowed individuals to survive up to this point, and any change may be less beneficial rather than more. While some change and flexibility can be good, especially if an animal can build upon its already-learned skills (Seed & Boogert, 2013), too much, or too rapid, change can lead to negative

consequences (Berends, Goldring, Stein, & Cravens, 2010). For instance, there are drawbacks to changing faster than one's environment, or making changes in response to what may be fleeting ecological circumstances. Moreover, there may simply be high costs to innovating; a new solution may be equally (or more) likely to be detrimental than beneficial. For instance, a subordinate who lacks good access to food may eat something poisonous while trying out a novel food source. All of these possibilities suggest that a certain level of hesitancy to adopting novel behaviours is warranted.

Research thus far indicates that individuals primarily innovate if their existing behaviour pattern no longer provides a benefit or when an individual has no other option. Therefore, the most likely innovators are those for whom the benefits of increased resources are the highest. For example, Laland and Reader (1999a) found that among guppies, *Poecilia reticulata*, innovation was seen in smaller individuals more than larger ones, and in females (for whom fecundity is limited by body size and condition, such that increased resources are directly tied to increased reproductive output), but not males (for whom there is no such link). But innovation may not occur even in situations in which it would be a substantial benefit. Why, then, would individuals fail to innovate

* Correspondence: S. F. Brosnan, Department of Psychology, Georgia State University, P.O. Box 5010, Atlanta, GA 30302, U.S.A.

E-mail address: sbrosnan@gsu.edu (S. F. Brosnan).

in a circumstance like this, where the potential benefits outweigh the potential risks? One barrier to innovation may be a number of evolved behavioural propensities, or psychological mechanisms, that influence behaviour in consistent ways. It is these psychological mechanisms that we consider below.

Here, we follow a global definition of innovation, including processes from the moment of discovery through establishment (Reader & Laland, 2003). We include in our considerations both the discovery of a novel behaviour to solve a problem and the application of an existing behaviour to a novel situation (van Horik, Clayton, & Emery, 2012; Ramsey, Bastian, & van Schaik, 2007). Within this definition, we follow a framework from anthropology that identifies three key phases to innovation: invention, transmission and preservation (Erwin, 2004; Mesoudi & O'Brien, 2008a, 2008b; Rose & Felton, 1955). The first of these, invention, is the creation of a novel behaviour or technology. The second phase is transmission, in which the invention spreads to other individuals through social means (Hoppitt & Laland, 2013). The third phase is preservation, in which a sufficiently large number of individuals adopt the invention that the behavioural variation is maintained in the social group (note that as a result of chance and competing pressures, even beneficial inventions often do not become widespread; Kummer & Goodall, 1985; Nishida, Matsusaka, & McGrew, 2009; Reader & Laland, 2003). Because our focus is on the psychological mechanisms that limit invention and transmission, we also focus on larger-brained, group-living species, including nonhuman primates (hereafter, primates), birds and fish.

In this review, we consider five psychological mechanisms that may inhibit both invention and transmission: (1) neophobia (a hesitancy to approach a novel object, locale or food item; Greenberg, 2003), (2) conservatism (the disinclination to explore/adopt new possibilities or opportunities; Hrubesch, Preuschoft, & van Schaik, 2009), (3) conformity (the tendency to do what your peers do; Boyd & Richerson, 1985), (4) functional fixedness (the disinclination to use familiar objects in novel ways; Hanus, Mendes, Tennie, & Call, 2011) and (5) the endowment effect (the bias towards preferring an existing option over a new one; Jones & Brosnan, 2008; also see Appendix, Table A1). The feature common to each of these mechanisms is that individuals tend to stick with familiar behaviours, and the existing uses of those behaviours, rather than exploring novel options. We additionally consider how certain transmission biases (Laland, 2004) and social learning mechanisms (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009) may inhibit, rather than encourage, the transmission and preservation of novel behaviours among animals. Although we have chosen to focus on how these limit innovation, this is within a framework of considering the trade-offs that exist for any of these behaviours. Thus, throughout we also consider the benefits that these psychological mechanisms may provide.

PSYCHOLOGICAL MECHANISMS THAT MAY LIMIT INNOVATION

Neophobia

Recent research has begun to demonstrate interindividual differences but intraindividual consistency in animals' innovative ability (Laland & Reader, 1999b; Morand-Ferron, Cole, Rawles, & Quinn, 2011; Thornton & Samson, 2012), indicating a link between innovation and personality (Hopper et al., in press; Massen, Antonides, Arnold, Bionda, & Koski, 2014). One classic example of this link is that bold individuals (i.e. those who are less neophobic) may be more likely to innovate than others because they are more likely to explore novel objects or explore in novel situations, something that may covary with rank (Boogert, Reader, & Laland,

2006; Greenberg, 2003). One prominent manifestation of intra-species differences in neophobia occurs during foraging; animals that are highly neophobic are less likely to innovate and exploit new food resources. Food neophobia is common in omnivores, which must be appropriately hesitant in trying novel foods (to avoid negative consequences from poisonous or otherwise unpalatable foods). Although a certain level of caution may protect animals, it also reduces their ability to exploit novel food sources and so animals must be flexible in their responses. For example, although rhesus macaques, *Macaca mulatta*, show food neophobia (Johnson, 2000), they are less neophobic towards more desirable foods with a high sugar content (Johnson, 2007). One way that socially living animals can circumvent individual neophobia, which may increase their chances of survival, is through social influences, such as acquiring information about novel foods from conspecifics (Chiarati, Canestrari, Vera, & Baglione, 2012; Galef, 2001; Gustafsson, Krief, & Saint Jalme, 2011).

Not only does neophobia influence an animal's likelihood to explore new foods, but individual differences in boldness may also interact with the speed at which individuals can learn new skills (Teblich, Stankewitz, & Teschke, 2012). Indeed, in a recent study with caviies, *Cavia aperea*, bolder, more active and more aggressive animals were faster learners on a novel task, but less aggressive animals paid more attention to stimuli changes and were therefore better at the reversal learning task (Guenther, Brust, Dersen, & Trillmich, 2014). If there is a negative correlation between neophobia and learning speed, it seems likely that neophobia interacts with innovation in two ways. First, less neophobic individuals may be more likely to invent, as they are less inhibited in their exploration of a novel object. On the other hand, these less neophobic individuals may also be less likely to benefit from the transmission of an invention (see below for more discussion of transmission), as they are less likely to change an existing behavioural pattern.

Conservatism

Conservatism is the disinclination to explore or adopt novel solutions to problems when a productive one is already known (Hrubesch et al., 2009). Conservatism protects individuals against the costs of a failed exploration, but also reduces the likelihood of both invention and the transmission of inventions. Conservative individuals may fail to explore alternate approaches to a problem as long as the solution that they already know is providing some benefit. For instance, in foraging tasks, it may be that individuals do not innovate until they are unable to acquire food through known mechanisms, for example, because the food is not available (e.g. a seasonal fruit) or because the food is being monopolized by another individual (Boesch, 2013). This explanation has been posited to explain why lower-ranking individuals are likely to innovate (Katzir, 1983; Reader & Laland, 2001; Sigg, 1980); they are driven beyond their inherent conservatism because their currently known solution is not providing any, or enough, benefit (Hopper, Schapiro, Lambeth, & Brosnan, 2011). In two recent experiments, captive chimpanzees were presented with novel problem-solving tasks that could be solved in more than one manner to obtain food rewards (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008). In both studies, after subjects learned one solution, they failed to explore alternative solutions, and were thus classed as 'conservative' (see also Dean, Kendal, Schapiro, Thierry, & Laland, 2012).

More recent studies, however, have shown flexible, non-conservative learning by apes (Hopper et al., in press; Lehner, Burkart, & van Schaik, 2011; Manrique, Völter, & Call, 2013; Tonooka, Tomonaga, & Matsuzawa, 1997). For instance, Manrique et al. (2013) presented chimpanzees, *Pan troglodytes*,

with a tube containing a grape. In the first instance, a chimpanzee could remove the grape either by inserting its finger into a hole on the front of the tube and prising up the grape ('fingering'), or by pushing up a piston from the bottom of the tube ('lifting'). Both actions forced the grape up and out of the tube. In this first presentation, all the chimpanzees' responses were classed as 'fingering'. However, when the task was re-presented with the hole relocated further up the tube, rendering the 'fingering' technique unproductive, 67% of the chimpanzees' responses were recorded as 'lifting' (the profitable technique of pushing up the piston to obtain the grape). Thus, the chimpanzees were not stuck using the 'fingering' technique, but were able to adapt to changes in their environment and adopt a new successful strategy applying their knowledge about how to interact with the apparatus. Corvids, too, can apply previously learned knowledge about a foraging task to successfully solve the puzzle when the complexity of the task increases (von Bayern, Heathcote, Rutz, & Kacelnik, 2009).

We note, however, that when Manrique et al. (2013) presented the chimpanzees with the second puzzle, 27% of their responses were still classed as 'fingering', showing that they were not able to switch completely away from their previously used, and previously successful, method, even when it was no longer viable. Moreover, the chimpanzees did not reject their original technique until it was no longer useful, at which time they were 'forced' to innovate, indicating that the threshold to overcome conservatism may be rather high (see also Lehner et al., 2011). Thus, it appears that primates will preferentially use their personal information unless there is some reason not to do so, such as when it is costly to collect or use it, or when it is unreliable or outdated (Carter, Marshall, Heinsohn, & Cowlshaw, 2013; Kendal, Coolen, van Bergen, & Laland, 2005; Laland, 2004).

Conformity

Conformity, defined as 'copying the majority' (Boyd & Richerson, 1985), describes circumstances in which the likelihood of an individual adopting a behaviour increases with the number of individuals displaying it (Laland, 2004; Whiten, Horner, & De Waal, 2005). Although few experimental studies have tested 'copy the majority' conformity, experimental research has shown such conformity in some ape (Haun, Rekers, & Tomasello, 2012) and fish (Pike & Laland, 2010) species. We note, however, that in the social psychology literature, conformity refers to the act of going against one's personal knowledge in order to align with a peer or peers (Haun & Tomasello, 2011; Van Leeuwen, Cronin, Schütte, Call, & Haun, 2013). Typically, this also involves 'copying the majority' (cf. Asch, 1952, 1955) but it can also refer to 'copying a minority' (Moscovici, Lage, & Naffrechoux, 1969; reviewed in Maass & Clark, 1984). Although such conformity has traditionally been studied in humans, evidence for such conformity also exists for animals (Galef & Whiskin, 2008; Sherwin, Heyes, & Nicol, 2002; van de Waal, Borgeaud, & Whiten, 2013). Here, we consider conformity as copying the majority.

In nonhuman species, there is evidence that individuals will conform to the group's behaviour. For example, foraging decisions in nine-spined stickleback, *Pungitius pungitius*, are influenced by the number of other fish feeding at a given location (Pike & Laland, 2010). In addition, while immigrating female chimpanzees (*P. t. schweinfurthii*) at Mahale Mountains National Park, Tanzania, readily adopted the majority behaviours of their new group, novel inventions by individuals within the group were unlikely to become widely performed among the group, again indicating a tendency to conformity (Nishida et al., 2009; see also Luncz & Boesch, 2014). This may even be the case in situations in which

individuals have personally experienced the benefit of an alternate behaviour (Hopper et al., 2011; but see Van Leeuwen et al., 2013). In a study with captive chimpanzees, Hopper et al. (2011) reported that individuals continued to exchange plastic tokens with a researcher for low-value food items (pieces of carrot), despite gaining personal experience that exchanging an alternative token type would gain them much more desirable food rewards (grapes). This was presumably because the token associated with the low-value food was exchanged by the majority of their group, a behaviour that was initiated by a dominant individual. If so, then the chimpanzees' behaviour of 'copying the majority' might also be described by other transmission biases, such as 'copy successful individuals' or 'copy good social learners' (cf. Laland, 2004; see also Horner, Proctor, Bonnie, Whiten, & de Waal, 2010).

This last study nicely highlights the interplay between conformity and conservatism; even after a beneficial new behaviour is discovered, it may be negatively influenced by conformity and thus not be adopted. As with conservatism, there are benefits to conformity (Over & Carpenter, 2013; Tennie, Call, & Tomasello, 2009; de Waal, 2001, 2013), but it may limit innovation in two ways. First, invention may be stifled by the tendency to do what everyone else does, rather than exploring and investigating new opportunities. For instance, if a new food source becomes available, individuals may fail to explore it because no other group members have done so. This has advantages, of course, as the new food source may be dangerous, but without an inventor, new niches may not be identified and individuals may miss out on opportunities for gain. Second, conformity may limit the transmission of inventions if individuals are not inclined to alter their behaviour away from the group norm. Thus, even if new behaviours emerge, they may be unable to spread, despite being beneficial (Hopper et al., 2011; Matsuzawa & Yamakoshi, 1996; Nishida et al., 2009; Sawyer & Robbins, 2009).

Functional Fixedness

Individuals can innovate by either applying existing solutions to new problems or creating new solutions for existing problems (Kummer & Goodall, 1985). A failure to achieve the latter is conservatism (discussed above), while a failure to achieve the former is 'functional fixedness' (Hanus et al., 2011; Manrique et al., 2013). Thus, while conservatism describes when an animal becomes 'stuck' on a particular strategy, functional fixedness describes the inability to develop or conceive of a new use for an existing behaviour or tool (Gruber, Muller, Reynolds, Wrangham, & Zuberbühler, 2011).

In the first paper to address this in detail, chimpanzees and children attempted to get a peanut from the bottom of a narrow tube, which could only be obtained by filling the tube with water so that the peanut floated to the top. In this study, the children had to discern that they needed to pour water from a watering can (initially used with the children for its intended purpose, watering plants) into the tube. The chimpanzees had to learn to obtain water from their water dispensers in their mouths without swallowing it, carry it to the tube and spit the water into the tube. None of the chimpanzees succeeded (Hanus et al., 2011). However, in another, related, study, one chimpanzee was able to get the peanut after having been provided with a new water source (i.e. not one that they had previously been used for drinking; Tennie, Call, & Tomasello, 2010). Thus, Hanus and colleagues hypothesized that the chimpanzees may have been unable to apply use of their drinking dispenser to solve the task (functional fixedness) but would be successful in applying a new 'tool' (a novel water dispenser) to solve the task. To test this, they presented some of the chimpanzees with the task again, but with a novel water dispenser

present. While this did result in a few successes, the success rate was extremely low. As chimpanzees in other tests have been shown to use a single tool in different ways (Hopper et al., 2007; Yamamoto, Humle, & Tanaka, 2013), it is not clear whether the limiting factor for the chimpanzees in this study was functional fixedness or a failure to understand the task itself.

While the idea of functional fixedness has intuitive appeal, as noted by Hanus et al. (2011), there have only been a few studies that have attempted to directly test it in animals, and the majority have involved great apes (Gruber et al., 2011). Therefore, more research is required. Nevertheless, if functional fixedness is a widespread bias, it may limit invention by dampening the exploration of novel uses for existing objects. It could potentially affect transmission as well, if individuals are disinclined to use a novel object for a new purpose even after seeing the majority of the group benefit from the different usage. Again, this highlights the potential interplay between these limiting factors (in this case, functional fixedness and conformity). If functional fixedness does turn out to be an important limitation for animals, it will be important to distinguish whether the inflexibility is due to the difficulty of applying a known behaviour in a novel situation, or using an object with a known purpose for a novel one. Studies to date have focused on tool use and do not allow us to separate these possibilities.

The Endowment Effect

The endowment effect is the tendency for individuals to value what they currently possess more than an alternate option, even if that alternate option is one that they would prefer in a free choice between the two (Kahneman, Knetsch, & Thaler, 1990, 1991). This means that individuals' preferences are altered by the mere possession of an item. The endowment effect has thus far only been tested in nonhuman primates (Brosnan et al., 2007; Brosnan, Jones, Gardner, Lambeth, & Schapiro, 2012; Drayton, Brosnan, Carrigan, & Stoinski, 2013; Flemming, Jones, Mayo, Stoinski, & Brosnan, 2012; Kanngiesser, Santos, Hood, & Call, 2011; Lakshminarayanan, Keith Chen, & Santos, 2008) using a procedure derived from human studies of the effect (Knetsch, 1989). It is related to loss aversion, a phenomenon in which people are more averse to losses than to similarly sized gains (Johnson, Gachter, & Herrmann, 2006; Kahneman et al., 1991), although in both cases what needs to be explained is why individuals show this aversion towards a loss when the potential gains outweigh the value of the object in question (Jones & Brosnan, 2008). There is also evidence for loss aversion in capuchin monkeys, *Cebus apella* (Chen, Lakshminarayanan, & Santos, 2006), although procedural questions in that study urge caution in the interpretation of the results (Silberberg et al., 2008).

In animals, the endowment effect is typically demonstrated by establishing subjects' preference between two foods in a dichotomous choice paradigm and then, on separate trials, giving each subject food and establishing whether or not it will trade for the alternative option. Control conditions are used to rule out that subjects simply like to trade (i.e. they are given an object and offered the chance to trade for an identical object) and that they are unwilling to give up an object, especially food, for any other object (i.e. subjects are given a very low-value food and offered the opportunity to trade for a higher-value one; even subjects that show an endowment effect should be willing to trade for a much better item). Subjects are considered to have an endowment effect if they keep *both* the food that they prefer and the one that they do not prefer. In addition, animals have been tested in a within-subjects design that demonstrates the relative prevalence of the endowment effect within a species (e.g. Brosnan et al., 2007; Drayton et al., 2013; Flemming et al., 2012).

From an evolutionary perspective, this bias is quite logical; if individuals are living in a risky environment, in which exchanges or transfers have a high probability of not being completed, then the risk of losing both objects must be considered in calculating the cost of the exchange (presumably this calculation is unconscious in other species and, in many cases, in humans). If this risk is sufficiently high, then it outweighs the potential benefit of the more preferred object. Supporting this evolutionary argument, a greater proportion of apes show endowment effects for foods, which may be limited, than for objects (in these cases, toys), possibly indicating a stronger bias to keep items that are more relevant for survival (Brosnan et al., 2007; Drayton et al., 2013; Flemming et al., 2012; Kanngiesser et al., 2011). Chimpanzees also show an endowment effect for tools, but only when the tools can be used to obtain foods that are immediately available; they fail to show an endowment effect for the same tools when the foods are present but are not immediately available (Brosnan et al., 2012). This may indicate that the bias is not due to the item *per se*, but what the item is worth.

As with the aforementioned mechanisms, particularly conservatism and conformity, a preference to retain a known entity rather than acquire a novel commodity or engage in a novel behaviour will limit innovation. While conservatism is a failure to explore because of the risks inherent in the exploration, the endowment effect is a failure to explore because of the risks of losing what an animal currently has. Although these may result in similar outcomes, the underlying mechanisms differ. Conformity involves engaging in the same behaviour as one's conspecific groupmates, which, again, differs from the mechanism for the endowment effect, but results in a similar functional outcome. We highlight these nuances because, despite the fact that the outcomes of these different biases may be similar, in order to make strong predictions about innovation (or the lack thereof) we need to understand the specific reasons why individuals may or may not innovate. Thus, understanding these underlying mechanisms accurately is critical in advancing our understanding of innovation in animals.

CONSIDERING THE SOCIAL ENVIRONMENT: LIMITATIONS TO TRANSMISSION AND MAINTENANCE OF INVENTIONS

Social Learning Mechanisms

When an individual learns from the actions of another, whether directly or indirectly, the method of this transmission can be classed as one of a number of social learning mechanisms which, in turn, can both inhibit and facilitate their spread and maintenance (Young, 2009). In contrast to transmission biases that describe 'when' and 'who' an animal copies (see *Transmission Biases and the Spread of Innovations* below), social learning mechanisms describe 'what' an animal copies. At the simplest level, the mere presence of conspecifics may encourage animals to be less neophobic and more exploratory, leading to greater innovation (Coleman & Mellgren, 1994) and the discovery of new behaviours or resources (Chiarati et al., 2012; Dindo, Whiten, & de Waal, 2009; Hopper, Holmes, Williams, & Brosnan, 2013). It is well documented, for example, that animals will be more likely to begin eating novel foods if they observe another individual eating that food (Stöwe et al., 2006; Zajonc, 1965), especially if the other animal is a familiar individual (Figuroa, Solà-Oriol, Manteca, & Pérez, 2013; Swaney, Kendal, Capon, Brown, & Laland, 2001). However, it has been proposed that social facilitation and local enhancement (when an animal's attention is drawn to a novel locale by the presence of conspecifics) are not sufficient for the transmission of complex behavioural innovations. In such a circumstance, no new behaviour is replicated,

but instead, individuals discover the behaviour themselves (Boyd & Richerson, 1996). Homogenous traditions may still emerge as a result of environmental and behavioural constraints (Acerbi, Jacquet, & Tennie, 2012).

Beyond such 'simple' mechanisms, animals may learn a behaviour either by recreating the goal, or end-state, that they observed a conspecific perform (emulation), or by replicating all aspects of the behaviour faithfully, including both the end-state and the actions to reach that end-state (imitation; Hopper, 2010). We note this distinction as it has been proposed that only through imitating can individuals faithfully replicate behaviours (Gergely & Csibra, 2006), which also encourages the accumulation of skills leading to complex cumulative culture (Dean, Vale, Laland, Flynn, & Kendal, 2013). This is because actions that are actually essential may appear irrelevant (i.e. the necessity of turning a key once it is in the ignition to start one's car; one need not understand the causal chain of these actions, but must simply imitate them to successfully reach the end-state of starting the car). Nevertheless, despite allowing for high-fidelity replication, imitation is unlikely to, in and of itself, be sufficient for behaviours to be maintained over time (Claidière & Sperber, 2010). Indeed, experimental work with chimpanzees has shown that, while they may be able to faithfully copy the behaviour of another (Whiten et al., 2005; but see Tennie, Call, & Tomasello, 2012), over time individuals explore alternative techniques, and these subsequent innovations lead to behavioural 'corruptions' (Hopper et al., 2007; Tennie et al., 2009). Although such exploratory behaviour may disrupt maintenance of behaviours over time, it is important because if individuals 'blindly' imitate and replicate, there may be fewer inventions because of decreased exploration.

Emulation may be more likely to encourage innovation by individuals. When animals emulate, they replicate the same goal or end-state, but develop their own novel method to achieve that goal (Wood, 1989); they are not preserving the invention precisely. The efficacy of emulation for transmission and maintenance of inventions, however, may depend on the information that needs to be passed on. Although the transmission of innovations may be limited if the inventor is no longer present (because of reduced opportunities for social learning), learning by emulation does not always require such direct observations. Because emulation describes the replication of end-states, if the invention pertains to a physical object (e.g. an anvil for cracking nuts), then naïve group members may be able to replicate the invention from its products, without ever needing to observe a model (Caldwell, Schillinger, Evans, & Hopper, 2012; Tomasello, 1999). Actions, gestures and other behavioural traditions, however, certainly cannot be transmitted via emulation as no product (end-state) remains from which the observer could learn (Caldwell & Millen, 2009). For example, in 2006 a 6-year-old female gorilla, *Gorilla gorilla beringei*, living in Bwindi Impenetrable National Park, Uganda, was recorded to invent a novel and effective technique for processing prickly thistles prior to eating them (Sawyer & Robbins, 2009). However, as this female emigrated from her group within 6 months of making this discovery, there were not sufficient opportunities for others in her group to learn this new technique from observing her and no other gorillas developed the behaviour (Sawyer & Robbins, 2009).

Transmission Biases and the Spread of Innovations

Thus far we have considered how an individual's characteristics may inhibit their ability to innovate or to adopt new behaviours invented by others, but to understand these limitations, and also the factors that limit the maintenance of novel behaviours within a social group, we must also consider the interplay between an

individual and their social environment. There are numerous ways in which the spread of inventions may be inhibited, but at the simplest level there may not be sufficient opportunities for the transfer of information. For example, the inventor may no longer be available for others to observe (Sawyer & Robbins, 2009). Even if the inventor is present, the social landscape may not be conducive for an individual to acquire the new information because individuals within the group are not equally connected (Leca, Gunst, Watanabe, & Huffman, 2007; Pradhan, Tennie, & van Schaik, 2012; Rose & Felton, 1955). For instance, if an inventor is very low ranking or peripheral, others may not notice the invention (Biro et al., 2003; Matsuzawa & Yamakoshi, 1996). Conversely, low-ranking or peripheral individuals may not be able to get close enough to high-ranking individuals to learn about beneficial inventions made by dominants (Dindo, Theiry, de Waal, & Whiten, 2010; Hopper et al., 2013), or their low rank might inhibit their ability to exploit the invention (Drea & Wallen, 1999).

In addition, observed information may conflict with an individual's personal information (Mesoudi, 2010) or, in an uncertain environment, observers may not be certain who or what to copy (Carter et al., 2013; Kendal et al., 2005). Therefore, animals must be selective about the social information they adopt, considering when to rely on social information and which individuals they should copy. Such decision making is described as transmission biases (Morgan, Rendell, Ehn, Hoppitt, & Laland, 2011; Rendell et al., 2011) or social learning strategies (Laland, 2004). As social learning may not always be the optimal option (Giraldeau, Valone, & Templeton, 2002), Laland (2004) argued that natural selection would have favoured biases to enable animals to determine when to best exploit social information. Thus, transmission biases should not only predict when inventions should arise, but also whether and how inventions will be transmitted and maintained within a group.

A social group of animals is not a homogenous unit, but is made up of animals that are differentially related, which may both facilitate or hinder innovation and transmission. For chimpanzees, for example, it has been proposed that increased physical proximity between certain individuals correlates with the transmission of an innovation (Bonnie & de Waal, 2005), such that individuals who affiliate less often will be less able to garner new information from one another. Thus, being a group member is not sufficient; an individual might also need to be closely affiliated with the inventor. Typically, interindividual relationships within social groups can be described by more than proximity, and are influenced by age (Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001), kinship (Tóth et al., 2009), and even personality (Massen & Koski, 2014), all of which may influence information transmission. Kin relationships may be particularly important as kin may have greater access to innovators than others, hence biasing the spread of innovations (Leca et al., 2007). For example, in a field experiment in which a group of wild vervet monkeys, *Chlorocebus aethiops*, was presented with grapes covered in sand, the monkeys developed techniques for cleaning the grapes prior to eating them (van de Waal, Krützen, Hula, Goudet, & Bshary, 2012). However, the monkeys socially learned specific techniques from their mothers (i.e. following the transmission bias 'copy kin'; Laland, 2004), which resulted in the different matrilineal lines using distinct food-processing techniques. The confinement of techniques within matrilineal lines may limit cultural transmission throughout the group and, therefore, the broader spread of innovations (Tanaka, 1998; van de Waal et al., 2012). In fact, for humans, it has been proposed that females may actively propagate their behaviours to kin (Avital & Jablonka, 1994). This would indicate that behavioural transmission may be maintained by kin selection, perhaps increasing similarity within kin groups as compared to the entire

population (Henrich & Henrich, 2010). Given the ubiquity of kin selection (e.g. Browning, Patrick, Rollins, Griffith, & Russell, 2012; Silk, 2001; Strassmann, Page, Robinson, & Seeley, 2011; Widdig et al., 2001), 'copy kin' biases are likely widespread in animals.

CONCLUSION

We end by reiterating that, while certain of these biases limit innovation by reducing exploration and experimentation, all provide benefits as well. As with all dynamic systems, a balance is required between innovation of the new and maintenance of the old, both across and within individuals. These psychological mechanisms represent a part of the balance that must be struck between the number of innovators and social learners in a group and the rate at which individuals innovate (Giraldeau, Caraco, & Valone, 1994). Perhaps only when individuals are forced through circumstances to explore alternative strategies will they do so (Boesch, 2013; Kummer & Goodall, 2003; Laland & Reader, 1999a; Lee, 2003; Lehner et al., 2011; Reader & MacDonald, 2003), and whether the resulting inventions are maintained depends on an interplay between the individual and their physical and social environment.

Acknowledgments

We thank Joan Strassmann for organizing a symposium on Bill Hamilton's legacy for her President's Symposium at the 50th Animal Behavior meeting in Boulder, Colorado in 2013. The seeds of this paper began in 2012 when S.F.B. was asked to give a talk on innovation in non-humans at the Squaw Valley meeting for the Gruter Institute for Law and Behavioral Research. At that meeting, and the subsequent 2013 meeting, when S.F.B. spoke again on the topic, conversations with the other attendees further developed our thinking. We thank them for their insightful comments. Lastly, we acknowledge support from the National Science Foundation (NSF CAREER Award SES 0847351, NSF HSD grant SES 0729244 and NSF SES 1123897 to S.F.B.) and the Leo S. Guthman Foundation (to L.M.H.) during the writing of this paper.

References

- Acerbi, A., Jacquet, P. O., & Tennie, C. (2012). Behavioral constraints and the evolution of faithful social learning. *Current Zoology*, *58*, 307–318.
- Asch, S. E. (1952). *Social psychology*. Englewood Cliffs, NJ: Prentice Hall.
- Asch, S. E. (1955). Opinions and social pressure. *Scientific American*, *193*, 31–35.
- Avital, E., & Jablonka, E. (1994). Social learning and the evolution of behaviour. *Animal Behaviour*, *48*, 1195–1199.
- von Bayern, A. M. P., Heathcote, R. J. P., Rutz, C., & Kacelnik, A. (2009). The role of experience in problem solving and innovative tool use in crows. *Current Biology*, *19*, 1965–1968.
- Berends, M., Goldring, E., Stein, M., & Cravens, X. (2010). Instructional conditions in charter schools and students' mathematics achievement gains. *American Journal of Education*, *116*, 303–335.
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, *6*, 213–223.
- Boesch, C. (2013). Ecology and cognition of tool use in chimpanzees. In C. M. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 21–47). New York, NY: Cambridge University Press.
- Bonnie, K. E., & de Waal, F. B. M. (2005). Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates*, *47*, 27–34.
- Boogert, N. J., Reader, S. M., & Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, *72*, 1229–1239.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy*, *88*, 77–93.
- Brosnan, S. F., Jones, O. D., Gardner, M., Lambeth, S. P., & Schapiro, S. J. (2012). Evolution and the expression of biases: situational value changes the endowment effect in chimpanzees. *Evolution and Human Behavior*, *33*, 378–386.
- Brosnan, S. F., Jones, O. D., Lambeth, S. P., Mareno, M. C., Richardson, A. S., & Schapiro, S. J. (2007). Endowment effects in chimpanzees. *Current Biology*, *17*, 1704–1707.
- Browning, L. E., Patrick, S. C., Rollins, L. A., Griffith, S. C., & Russell, A. F. (2012). Kin selection, not group augmentation, predicts helping in an obligate cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 3861–3869.
- Caldwell, C. A., & Millen, A. E. (2009). Social learning mechanisms and cumulative cultural evolution: is imitation necessary? *Psychological Science*, *20*, 1478–1483.
- Caldwell, C. A., Schillinger, K., Evans, C. L., & Hopper, L. M. (2012). End state copying by humans (*Homo sapiens*): implications for a comparative perspective on cumulative culture. *Journal of Comparative Psychology*, *126*, 161–169.
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlshaw, G. (2013). Personality predicts decision making only when information is unreliable. *Animal Behaviour*, *86*, 633–639.
- Chen, M. K., Lakshminarayanan, V., & Santos, L. R. (2006). How basic are behavioral biases? Evidence from capuchin monkey trading behavior. *Journal of Political Economy*, *114*, 517–537.
- Chiariati, E., Canestrari, D., Vera, R., & Baglione, V. (2012). Subordinates benefit from exploratory dominants: response to novel food in cooperatively breeding carion crows. *Animal Behaviour*, *83*, 103–109.
- Claidière, N., & Sperber, D. (2010). Imitation explains the propagation, not the stability of animal culture. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 651–659.
- Coleman, S. L., & Mellgren, R. L. (1994). Neophobia when feeding alone or in flocks in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, *48*, 903–907.
- Dawkins, R. (2000, 10 March). Obituary for W.D. Hamilton. *The Independent* (London).
- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*, 1114–1118.
- Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2013). Human cumulative culture: a comparative perspective. *Biological Reviews*. <http://dx.doi.org/10.1111/brv.12053>. Advance online publication.
- Dindo, M., Thierry, B., de Waal, F. B. M., & Whiten, A. (2010). Conditional copying fidelity in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *124*, 29–37.
- Dindo, M., Whiten, A., & de Waal, F. B. M. (2009). Social facilitation of exploratory foraging behavior in capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, *71*, 419–426.
- Drayton, L., Brosnan, S. F., Carrigan, J., & Stoinski, T. S. (2013). Endowment effects in gorillas (*Gorilla gorilla*). *Journal of Comparative Psychology*, *127*, 365–369.
- Drea, C. M., & Wallen, K. (1999). Low-status monkeys 'play dumb' when learning in mixed social groups. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 12965–12969.
- Erwin, D. H. (2004). Evolution: insights into innovation. *Science*, *304*, 1117–1119.
- Figueroa, J., Solà-Oriol, D., Manteca, X., & Pérez, J. F. (2013). Social learning of feeding behaviour in pigs: effects of neophobia and familiarity with the demonstrator conspecific. *Applied Animal Behaviour Science*, *148*, 120–127.
- Flemming, T. M., Jones, O. D., Mayo, L., Stoinski, T., & Brosnan, S. F. (2012). The endowment effect in orangutans. *International Journal of Comparative Psychology*, *25*, 285–298.
- Galef, B. G. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, *61*, 3–15.
- Galef, B., & Whiskin, E. (2008). 'Conformity' in Norway rats? *Animal Behaviour*, *75*, 2035–2039.
- Gergely, G., & Csibra, G. (2006). Sylvia's recipe: the role of imitation and pedagogy in the transmission of cultural knowledge. In N. J. Enfield, & S. C. Levinson (Eds.), *Roots of human sociality: Culture, cognition, and human interaction* (pp. 229–255). Oxford, U.K.: Berg.
- Giraldeau, L.-A., Caraco, T., & Valone, T. J. (1994). Social foraging: individual learning and cultural transmission of innovations. *Behavioral Ecology*, *5*, 35–43.
- Giraldeau, L.-A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*, 1559–1566.
- Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour in birds. In R. Greenberg, S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 175–196). New York, NY: Oxford University Press.
- Gruber, T., Muller, M. N., Reynolds, V., Wrangham, R., & Zuberbühler, K. (2011). Community-specific evaluation of tool affordances in wild chimpanzees. *Scientific Reports*, *1*, 128.
- Guenther, A., Brust, V., Dersen, M., & Trillmich, F. (2014). Learning and personality types are related in cavies (*Cavia aperea*). *Journal of Comparative Psychology*, *128*, 74–81.
- Gustafsson, E., Krief, S., & Saint Jalme, M. (2011). Neophobia and learning mechanisms: how captive orangutans discover medicinal plants. *Folia Primatologica*, *82*, 45–55.
- Hanus, D., Mendes, N., Tennie, C., & Call, J. (2011). Comparing the performances of apes (*Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*) and human children (*Homo sapiens*) in the floating peanut task. *PLoS One*, *6*, e19555.
- Haun, D. B. M., Rekers, Y., & Tomasello, M. (2012). Majority-biased transmission in chimpanzees and human children, but not orangutans. *Current Biology*, *22*, 727–731.

- Haun, D. B. M., & Tomasello, M. (2011). Conformity to peer pressure in preschool children: peer pressure in preschool children. *Child Development*, 82, 1759–1767.
- Henrich, J., & Henrich, N. (2010). The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proceedings of the Royal Society B: Biological Sciences*, 277, 3715–3724.
- Hopper, L. M. (2010). 'Ghost' experiments and the dissection of social learning in humans and animals. *Biological Reviews*, 85, 685–701.
- Hopper, L., Holmes, A., Williams, L., & Brosnan, S. (2013). Dissecting the mechanisms of squirrel monkey (*Saimiri boliviensis*) social learning. *PeerJ*, 1, e13.
- Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (in press). Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal Cognition*. <http://dx.doi.org/10.1007/s10071-013-0715-y>.
- Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, 81, 1195–1202.
- Hopper, L., Spiteri, A., Lambeth, S., Schapiro, S., Horner, V., & Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour*, 73, 1021–1032.
- Hoppitt, W., & Laland, K. N. (2013). *Social learning an introduction to mechanisms, methods, and models*. Princeton, NJ: Princeton University Press.
- van Horik, J. O., Clayton, N. S., & Emery, N. J. (2012). Convergent evolution of cognition in corvids, apes and other animals. In J. Vonk, & T. K. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp. 80–101). New York, NY: Oxford University Press.
- Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. M. (2010). Prestige affects cultural learning in chimpanzees. *PLoS One*, 5, e10625.
- Hrubesch, C., Preuschoft, S., & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition*, 12, 209–216.
- Johnson, E. (2000). Food-neophobia in semi-free ranging rhesus macaques: effects of food limitation and food source. *American Journal of Primatology*, 50, 25–35.
- Johnson, E. C. (2007). Rhesus macaques (*Macaca mulatta*) are not neophobic toward novel food with a high sugar content. *American Journal of Primatology*, 69, 591–596.
- Johnson, E. J., Gächter, S., & Herrmann, A. (2006). Exploring the nature of loss aversion [Institute for the Study of Labor (IZA) Discussion Paper No. 2015, Social Science Research Network, 2006]. Abstract retrieved from: <http://ssrn.com/abstract=892336>.
- Jones, O. D., & Brosnan, S. F. (2008). Law, biology & property: a new theory of the endowment effect. *William and Mary Law Review*, 49, 1935–1990.
- Kahneman, D., Knetsch, J. L., & Thaler, R. (1990). Experimental tests of the endowment effect and the Coase theorem. *Journal of Economic Perspectives*, 98, 1325–1348.
- Kahneman, D., Knetsch, J. L., & Thaler, R. (1991). Anomalies: the endowment effect, loss aversion, and status quo bias. *Journal of Economic Perspectives*, 5, 193–206.
- Kanngiesser, P., Santos, L. R., Hood, B. M., & Call, J. (2011). The limits of endowment effects in great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*). *Journal of Comparative Psychology*, 125, 436–445.
- Katzir, G. (1983). Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula* L. II. Response to novel palatable food. *Behaviour*, 87, 183–208.
- Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, 35, 333–379.
- Knetsch, J. L. (1989). The endowment effect and evidence of nonreversible indifference curves. *American Economic Review*, 79, 1277–1284.
- Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 308, 203–214.
- Kummer, H., & Goodall, J. (2003). Conditions of innovative behavior in primates. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 223–236). Oxford, U.K.: Oxford University Press.
- Lakshminarayanan, V., Keith Chen, M., & Santos, L. R. (2008). Endowment effect in capuchin monkeys. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3837–3844.
- Laland, K. N. (2004). Social learning strategies. *Learning and Behavior*, 32, 4–14.
- Laland, K. N., & Reader, S. M. (1999a). Foraging innovation in the guppy. *Animal Behaviour*, 57, 331–340.
- Laland, K. N., & Reader, S. M. (1999b). Foraging innovation is inversely related to competitive ability in male but not in female guppies. *Behavioral Ecology*, 10, 270–274.
- Leca, J.-B., Gunst, N., Watanabe, K., & Huffman, M. A. (2007). A new case of fish-eating in Japanese macaques: implications for social constraints on the diffusion of feeding innovation. *American Journal of Primatology*, 69, 821–828.
- Lee, P. C. (2003). Innovation as a behavioural response to environmental challenges: a cost and benefit approach. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 261–278). Oxford, U.K.: Oxford University Press.
- Lehner, S. R., Burkart, J. M., & van Schaik, C. P. (2011). Can captive orangutans (*Pongo pygmaeus abelii*) be coaxed into cumulative build-up of techniques? *Journal of Comparative Psychology*, 125, 446–455.
- Luncz, L. V., & Boesch, C. (2014). Tradition over trend: neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *American Journal of Primatology*. <http://dx.doi.org/10.1002/ajp.22259>. Advance online publication.
- Maass, A., & Clark, R. D. (1984). Hidden impact of minorities: fifteen years of minority influence research. *Psychological Bulletin*, 95, 428.
- Manrique, H. M., Völter, C. J., & Call, J. (2013). Repeated innovation in great apes. *Animal Behaviour*, 85, 195–202.
- Marshall-Pescini, S., & Whiten, A. (2008). Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Animal Cognition*, 11, 449–456.
- Massen, J. J. M., Antonides, A., Arnold, A.-M. K., Bionda, T., & Koski, S. (2014). A behavioural view on chimpanzee personality: exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *American Journal of Primatology*, 75, 947–958.
- Massen, J. J. M., & Koski, S. E. (2014). Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, 35, 1–8.
- Matsuzawa, T., & Yamakoshi, G. (1996). Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 211–232). Cambridge, U.K.: Cambridge University Press.
- Mesoudi, A. (2010). The experimental study of cultural innovation. In M. J. O'Brien, & S. J. Shennan (Eds.), *Innovation in cultural systems* (pp. 175–192). Cambridge, MA: MIT Press.
- Mesoudi, A., & O'Brien, M. J. (2008a). The cultural transmission of great basin projectile-point technology I: an experimental simulation. *American Antiquity*, 73, 3–28.
- Mesoudi, A., & O'Brien, M. J. (2008b). The cultural transmission of great basin projectile-point technology II: an agent-based computer simulation. *American Antiquity*, 73, 627–644.
- Morand-Ferron, J., Cole, E., Rawles, J., & Quinn, J. (2011). Who are the innovators? A field experiment with 2 passerine species. *Behavioral Ecology and Sociobiology*, 22, 1241–1248.
- Morgan, T. J. H., Rendell, L. E., Ehn, M., Hoppitt, W., & Laland, K. N. (2011). The evolutionary basis of human social learning. *Proceedings of the Royal Society B: Biological Sciences*, 279, 653–662.
- Moscovici, S., Lage, E., & Naffrechoux, M. (1969). Influence of a consistent minority on the responses of a majority in a color perception task. *Sociometry*, 32, 365–380.
- Nishida, T., Matsusaka, T., & McGrew, W. C. (2009). Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates*, 50, 23–36.
- Over, H., & Carpenter, M. (2013). The social side of imitation. *Child Development Perspectives*, 7, 6–11.
- Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, 6, 466–468.
- Pradhan, G. R., Tennie, C., & van Schaik, C. P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. *Journal of Human Evolution*, 63, 180–190.
- Queller, D. C. (2001). W. D. Hamilton and the evolution of sociality. *Behavioral Ecology*, 12, 261–264.
- Ramsey, G., Bastian, M. L., & van Schaik, C. (2007). Animal innovation defined and operationalized. *Behavioral and Brain Sciences*, 30, 393–437.
- Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age, and social rank differences. *International Journal of Primatology*, 22, 787–805.
- Reader, S. M., & Laland, K. N. (2003). Animal innovation: an introduction. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 3–38). Oxford, U.K.: Oxford University Press.
- Reader, S. M., & MacDonald, K. (2003). Environmental variability and primate behavioural flexibility. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 83–116). Oxford, U.K.: Oxford University Press.
- Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, 15, 68–76.
- Rose, E., & Felton, W. (1955). Experimental histories of culture. *American Sociological Review*, 20, 383–392.
- Sawyer, S. C., & Robbins, M. M. (2009). A novel food processing technique by a wild mountain gorilla (*Gorilla beringei beringei*). *Folia Primatologica*, 80, 83–88.
- Seed, A. M., & Boogert, N. J. (2013). Animal cognition: an end to insight? *Current Biology*, 23, R67–R69.
- Segerstråle, U. C. O. (2013). *Nature's oracle: The life and work of W. D. Hamilton*. Oxford, U.K.: Oxford University Press.
- Sherwin, C. M., Heyes, C. M., & Nicol, C. J. (2002). Social learning influences the preferences of domestic hens for novel food. *Animal Behaviour*, 63, 933–942.
- Sigg, H. (1980). Differentiation of female positions in hamadryas one-male-units. *Zeitschrift für Tierpsychologie*, 53, 265–302.
- Silberberg, A., Roma, P. G., Huntsberry, M. E., Warren-Boulton, F. R., Sakagami, T., Ruggiero, A. M., et al. (2008). On loss aversion in capuchin monkeys. *Journal of the Experimental Analysis of Behavior*, 89, 145–155.
- Silk, J. B. (2001). Grunts, girneys, and good intentions: the origins of strategic commitment in nonhuman primates. In R. M. Nesse (Ed.), *Evolution and the capacity for commitment* (pp. 138–157). New York, NY: Russell Sage Foundation.
- Stöwe, M., Bugnyar, T., Loretto, M.-C., Schloegl, C., Range, F., & Kotrschal, K. (2006). Novel object exploration in ravens (*Corvus corax*): effects of social relationships. *Behavioural Processes*, 73, 68–75.
- Strassmann, J. E., Page, R. E., Robinson, G. E., & Seeley, T. D. (2011). Kin selection and eusociality. *Nature*, 471, E5–E6.

Swaney, W., Kendal, J., Capon, H., Brown, C., & Laland, K. N. (2001). Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, 62, 591–598.

Tanaka. (1998). Social diffusion of modified louse egg-handling techniques during grooming in free-ranging Japanese macaques. *Animal Behaviour*, 56, 1229–1236.

Tebbich, S., Stankewitz, S., & Teschke, I. (2012). The relationship between foraging, learning abilities and neophobia in two species of Darwin's finches. *Ethology*, 118, 135–146.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 2405–2415.

Tennie, C., Call, J., & Tomasello, M. (2010). Evidence for emulation in chimpanzees in social settings using the floating peanut task. *PLoS One*, 5, e10544.

Tennie, C., Call, J., & Tomasello, M. (2012). Untrained chimpanzees (*Pan troglodytes schweinfurthii*) fail to imitate novel actions. *PLoS One*, 7, e41548.

Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, 83, 1459–1468.

Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.

Tonooka, R., Tomonaga, M., & Matsuzawa, T. (1997). Acquisition and transmission of tool making and use for drinking juice in a group of captive chimpanzees (*Pan troglodytes*). *Japan*, 39, 253–265.

Tóth, Z., Bókony, V., Lendvai, Á. Z., Szabó, K., Péntzes, Z., & Líker, A. (2009). Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks. *Behavioural Processes*, 82, 173–177.

Van Leeuwen, E. J. C., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. M. (2013). Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PLoS One*, 8, e80945.

de Waal, F. B. M. (2001). *The ape and the sushi master*. New York, NY: Basic Books.

de Waal, F. B. M. (2013). Animal conformists. *Science*, 340, 437–438.

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, 340, 483–485.

van de Waal, E., Krützen, M., Hula, J., Goudet, J., & Bshary, R. (2012). Similarity in food cleaning techniques within matriline in wild vervet monkeys. *PLoS One*, 7, e35694.

Whiten, A., Horner, V., & De Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437, 737–740.

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 2417–2428.

Widdig, A., Nürnberg, P., Krawczak, M., Streich, W. J., & Bercovitch, F. B. (2001). Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 13769–13773.

Wood, D. (1989). Social interaction as tutoring. In M. H. Bornstein, & J. S. Bruner (Eds.), *Interaction in human development* (pp. 59–80). Hillsdale, NJ: L. Erlbaum.

Yamamoto, S., Humle, T., & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: social learning of a more efficient tool-use technique. *PLoS One*, 8, e55768.

Young, H. P. (2009). Innovation diffusion in heterogeneous populations: contagion, social influence, and social learning. *American Economic Review*, 99, 1899–1924.

Zajonc, R. B. (1965). Social facilitation. *Science*, 149, 269–274.

Appendix

Table A1
Definition of terms

Term	Definition	Source
Asocial learning	When an individual learns a new behaviour or skill without learning from others (i.e. by trial-and-error learning)	Laland (2004)
Conformity	Tendency to do what your peers do, specifically the tendency to 'copy the majority'	Boyd and Richerson (1985)
Conservatism	Disinclination to explore/adopt new possibilities or opportunities	Hrubesch et al. (2009)
Emulation	Recreating a conspecific's goal, or the end-state of their behaviour, but not the actions to reach this goal or end-state	Wood (1989)
Endowment effect	Preferring an object more once it is in one's possession than prior to its possession	Jones and Brosnan (2008)
Functional fixedness	Disinclination to use familiar objects in novel ways	Hanus et al. (2011)
Imitation	Faithful replication of all aspects of a behaviour, including both the end-state and the actions to reach that end-state	Whiten et al. (2009)
Innovation	'A process that results in new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire'	Reader and Laland (2003, p. 14)
Invention	Creation of a novel behaviour or technology	Mesoudi (2010)
Neophobia	Hesitancy to approach a novel object, locale or food item	Greenberg (2003)
Preservation	Adoption and maintenance of an innovation within a group of animals	Reader and Laland (2003)
Social learning mechanisms	Collective term for ways in which animals learn behaviours performed by others (e.g. emulation or imitation); refers specifically to 'what' is replicated	Whiten et al. (2009)
Social learning strategies	Describes animals' decision making to determine when they should use social information and who they should copy (synonymous with 'transmission biases')	Laland (2004)
Transmission biases	Collective term for factors that dictate how new behaviours spread within a group; refers specifically to 'who' and 'when' animals should use social information (see also 'social learning strategies')	Rendell et al. (2011)
Transmission	Process by which an invention spreads to other individuals though social means (i.e. via social or observational learning)	Hoppitt and Laland (2013)