

# WHAT ANIMALS OTHER THAN PRIMATES CAN TELL US ABOUT HUMAN CULTURAL TRANSMISSION

*Kevin Laland, Alice Cowie and Tom Morgan*

## **Introduction**

To most social scientists, human culture is unique, and bears no comparison to the behavioural traditions observed in other animals. To a large extent this position is justified, since our species alone has created technologies that endlessly bring forth new innovations, allowing it to transform environments to unprecedented levels and thereby dominate the planet; not to mention humanity's extraordinary achievements in the sciences, arts, music and literature. Our success as a species is widely attributed to this capability for culture, through which we share adaptive knowledge, and fashion solutions to life's challenges (Boyd and Richerson 1985; Plotkin 1997). Yet the observation that a wide range of other animals are also capable of innovation and social learning (Heyes and Galef 1996; Laland and Galef 2009), albeit to a lesser degree, begs the question of exactly what it is that is special about the cultural capabilities of humans.

It is here that a comparative perspective can be of utility. Careful analyses of the cognitive capabilities and social behaviour of humans and other animals potentially allows researchers to characterize the truly unique aspects of human culture. This is no trivial matter, since history is littered with examples of claims along the lines of 'humans uniquely do X, or possess Y' (e.g. use tools, teach, imitate, exhibit referential communication, possess episodic memory) that

have subsequently fallen by the wayside when established in another species. Such comparisons of course also isolate features that humans share with other animals, which can be equally insightful, since they pave the way to studying animals as model systems that can illuminate human behaviour. Moreover, comparisons between humans and other animals help us to reconstruct the past, and determine how, and from where, human cultural capability evolved.

Before meaningful comparisons between the ‘cultures’ of humans and other animals can be made, we need to specify precisely what we mean by the term culture. Once again, this is no trivial matter, since it has proven extremely difficult for social scientists to derive a satisfactory consensual definition, or to find means to operationalize culture (Kroeber and Kluckholm 1952; Durham 1991). The definition that we adopt follows Laland and Hoppitt (2003): *Cultures are those group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information.* This broad definition is designed to encourage relevant comparative data to be collected, providing a framework with which to investigate the evolutionary roots of culture. In our view, a narrower definition, for instance, one that automatically restricted culture to humans, would not prove particularly useful, at least not to researchers interested in a comparative perspective. This is not only because the answer to the question of whether or not animals have culture would be a fait accompli; by definition, they would not. But in addition, this denotation would act as a barrier to understanding the evolutionary roots of culture. No light would be shed on how culture came into existence, nor on humans’ place in nature. Premature, over-exacting distinctions potentially jeopardize our ability to see relationships between culture-like phenomena in diverse taxa.

Interestingly, when a broad definition is adopted, it transpires that some of the strongest evidence for culture in non-human animals comes not from our nearest relatives, the primates, but from a handful of distantly related and disparate animals – a few birds, whales and fish species (Laland and Hoppitt 2003). For instance, the claims of culture in chimpanzees are hotly contested (Humble and Newton-Fisher, this volume), not least because it is unclear whether the observed behavioural variation, labelled ‘culture’ (Whiten et al. 1999), results from differential social learning, or from differences in ecology or genetics (Laland and Janik 2006). However, we describe below experimental studies on natural populations of fish and birds that clearly demonstrate that the species concerned exhibit behavioural traditions reliant on social learning, and where population differences cannot be attributed to confounding genetic or ecological factors (Warner 1988; Slagsvold and Wiebe 2007). Likewise, arguably the best evidence for

animal teaching is in meerkats (Thornton and McAuliffe 2006); for animal innovation, mental time-travel and cumulative culture, it is in birds (Clayton and Dickinson 1998; Hunt and Gray 2003; Emery and Clayton 2004; Lefebvre et al. 2004); and for vocal learning, it is in cetaceans (Rendell and Whitehead 2001). These observations become significant once we recognize the full gamut of tools offered by the comparative method.

Comparative analyses between species can allow inferences to be made about the attributes of species ancestral to humans, and allow us to understand the evolutionary history of the traits seen in modern man. In simple terms, this approach is reliant on detecting homologies that humans and closely related animals share. Naturally, the first points of comparison that spring to mind are with non-human primates, particularly the apes. Researchers are interested in our closest relatives because these species potentially exhibit homologous traits to humans, due to shared ancestry, or may perhaps exhibit precursors of unique human characteristics, such as language. Unfortunately, advocates of this approach sometimes pin too much weight on the chimpanzee–human comparison (or to a lesser extent, the other apes–human comparison) in the name of homology, reasoning that since the chimpanzee shares more genes with humans than do other species, such comparisons are likely to be especially insightful. In fact, a single comparison, such as human–chimpanzee, contributes a solitary datum to any attempt to identify reliable relationships between selective environments and adaptations. By and large, the comparative method has moved on since the 1950s, when such pairwise comparisons were pioneered by ethologists, such as Niko Tinbergen and Konrad Lorenz, to shed light on behavioural adaptations; famously, comparisons between black-headed gulls and kittiwakes suggested numerous differences, related to nest construction and chick and parental behaviour, that could be understood as adaptations to the differential risk of predation in ground- and cliff-nesting gulls (Cullen 1957; Tinbergen et al. 1962; Tinbergen 1963). At best, such comparisons serve to generate an evolutionary hypothesis: at worst, they are nothing more than a source of uninformed speculation. In the case of the gulls, further comparisons amongst closely related birds exposed to similar selection regimes were necessary to confirm the evolutionary relationships (Clutton-Brock and Harvey 1984). So it is with chimpanzee–human comparisons, which must be complemented by further comparisons in order to yield meaningful information.

Moreover, a single comparison is uninformative as to which characters are ancestral and which are derived. In principle, all of the differences between humans and chimpanzees could have evolved in the chimpanzee lineage since divergence from the common ancestor.

The assumption that all the relevant evolutionary change took place in the hominin lineage has been a constant source of error in theories of human evolution. Consider, for example, the recent work on *Ardipithecus*, which suggests that the common ancestor of humans and chimpanzees may not have been a knuckle-walker, and that researchers have been misled by a chimpanzee model (Lovejoy 2009). Researchers that fail to consider ancestral and derived traits are vulnerable to making errors. More generally, if researchers restrict themselves to a narrow comparison involving a very small number of species closely related to humans, they risk telling apparently plausible ‘just-so stories’ about human evolution.

Of course, just how wide a comparison across taxa is useful will depend very much on the question in hand. Comparative analyses of animal abilities suggest that some human behavioural and psychological traits have a long history. For instance, a capacity for associative learning may even have evolved in our invertebrate ancestors; an understanding of causal relationships may be common to both mammals and birds; much social behaviour, such as forming stable social bonds, developing dominance hierarchies, and an understanding of third-party social relationships, probably evolved in our pre-hominid primate ancestors; while a capacity for true imitation probably evolved in pre-hominid apes. The important point here is that the appropriate taxonomic group for comparative analysis is not inevitably restricted to primates.

In this chapter we concentrate on two further ways in which a wider taxonomic net allows light to be shed on human cultural transmission. First, animals can be used as model systems to better understand behavioural and cognitive processes shared with humans. In this case, non-primates frequently provide an opportunity for more rigorous investigation of cultural transmission as they can be more easily manipulated in an experimental setting. For instance, much of the experimental work on animal social learning carried out in our laboratory involves studies of fish and birds. That is because these animals offer practical advantages over many other vertebrates for the study of social learning. After all, the diffusion of innovations and animal traditions are group-level phenomena, and if they are to be studied reliably, researchers require not just replicate animals but replicate populations of animals. While it would be economically and practically challenging (not to mention ethically questionable) to set up large numbers of replicate populations of chimpanzees or Japanese macaques, it is extremely straightforward and cheap to set up large numbers of populations of small fish in the laboratory, and subject them to experimentation. Similarly, we have been able to set up small experimental populations of birds in which to carry out diffusion

studies. These practical advantages allow for multiple conditions and good statistical power, bringing experimental rigour to any social learning investigation. Of course, such practical advantages would be worthless if birds and fish were hopeless at social learning, or never innovated, but below we provide evidence that this is not the case. On the contrary, we will describe examples of learning strategies proposed by anthropologists, psychologists and economists as rules that humans deploy that we also observe in birds and fish.

The second means of using the comparative method is to seek to identify ecological, social or life-history characters that co-vary with cognitive and behavioural traits shared by humans and animals. While the mechanisms underlying learning across species are frequently non-homologous, there are parallels at a functional level, and these are potentially informative with respect to the ecological and social factors that favour the evolution of the attribute concerned. This allows inferences to be made about the ancestral function of, and selective environment favouring, human capabilities. This method is reliant on detecting analogous processes amongst humans and distantly related animal species. Analogy is at least as powerful a comparative tool as homology (Harvey and Pagel 1991). Evolutionary hypotheses are well supported when independently derived data repeatedly suggest that a particular selection pressure consistently favours a specific character. For instance, Dunbar's (1995) observed relationship between neocortex size and group size in primates is rendered all the more compelling by the observation that convergent evolution has generated the same patterns in carnivores and ungulates (Dunbar and Bever 1998; Shultz and Dunbar 2006). Researchers who restrict themselves to homology fail to utilize a valid and powerful source of comparative data. Below we describe how comparative analyses using non-human taxa can shed light on the ecological factors that promote reliance on culture, and the capabilities that underpin it.

In summary, researchers wishing to draw inferences about human evolution based on comparisons with other species would be well advised not to focus solely on the common chimpanzee, the apes, or even the primates; nor should they pick and choose a comparator species from any single taxon. Rather, we recommend that they utilize the full power of the modern comparative method, complete with its sophisticated statistical tools (Harvey and Pagel 1991), harnessing both homology and analogy to maximal effect. In this chapter we endeavour to illustrate each of these approaches, focusing on studies of social learning and cultural transmission in animals. We suggest that non-primates can make, and indeed have made, a valid contribution using both of these approaches.

## Use of Model Species

### ***The Concept of ‘Model Species’***

Model organisms are species that are studied by scientists hoping to further understanding of wider biological phenomena relevant to a range of species, including humans. Of course, different model organisms are used to answer different biological questions, but most have some features in common. These include ready availability and short generation times (to enable scientists to make use of large sample sizes and experimental replication), along with being relatively easy to maintain and manipulate in a controlled experimental setting.

The use of model organisms in such fields as medicine, developmental biology and genetics is well established. For instance, the African clawed frog (*Xenopus laevis*), which produces large embryos with a high tolerance for physical and pharmacological manipulation, has proven to be a useful study species for addressing questions about vertebrate development (Jones 2005); while the single-celled yeast (*Saccharomyces cerevisiae*) is frequently used as a tool for investigating the genetic control of cellular processes (Fields and Johnston 2005).

Just as these species have thrown light on human cell functioning and embryological development, so may the study of behaviour in selected animal species (including rats, pigeons and sticklebacks) provide us with insights into cultural transmission. We can use them, for instance, to illuminate our understanding of how information flows through populations, as well as to investigate the occurrence of various ‘types’ of social learning, and social learning ‘strategies’. Of course, if human social learning was completely different from that of other animals, any insights that model species could offer would be limited. However, as evidence suggests that this is far from the case, model species may well be of considerable use.

### ***The Problem with Primates***

When seeking to understand the evolutionary history of the processes involved in human cultural transmission – and what, if anything, makes us ‘unique’ – researchers can look not only at humans, but at other animals. Primates, being our closest relatives, may be the obvious choice. However, studying them – and obtaining firm evidence of their capacity for social information transfer – is often not easy. Different populations of wild chimpanzees, for example, are known to exhibit differences in their behavioural repertoires, the best-known of which is perhaps the distinct tool-using patterns seen in different groups (Whiten et al. 1999; Boesch 2003; Whiten et al. 2003). Some or all of these may be socially learnt: chimpanzees are undoubtedly capable of social learning (Whiten and Custance 1996), and experiments

with captive populations have shown that, when different groups are 'seeded' with a demonstrator trained to solve a foraging task using a particular method, other members of the group acquire and maintain the same method of solving it as that of their demonstrator (Hopper et al. 2007; Whiten et al. 2007; Horner and de Waal 2009). With respect to wild chimpanzees, however, there is no irrefutable evidence that the distinct behaviour seen in groups living at different sites can be attributed to social rather than genetic or ecological factors.

Take the process of chimpanzee 'ant dipping' as an illustration. Chimpanzees at one African study site (Gombe) collect ants to eat by holding a long 'wand' (stick) in one hand and wiping a ball of ants off it with the other (the 'pull through' method), while those at another site (Tai) use a 'direct mouthing' technique, whereby a short stick held in one hand is used to catch a smaller number of ants, which are then transferred straight to the mouth. A number of researchers (Boesch and Boesch 1990; McGrew 1992; Whiten et al. 1999) contend that this difference cannot be accounted for by ecological variation between the sites, but this is debatable. On studying chimpanzees at a location (Bossou) where both forms of ant dipping are employed, Humle and Matsuzawa (2002) discovered that the technique individuals used to obtain ants was strongly influenced by the nature of their prey, which varied substantially in density and aggressiveness, and suggested that 'chimpanzees could individually be shaped by biting insects to use the strategy that resulted in the fewest bites' (Laland and Hoppitt 2003: 153). Although more recent research (Mobius et al. 2008) has claimed that differences in ant behaviour are probably not sufficient to account for the differences seen in the ant-dipping methods used by chimpanzees at Gombe and Tai, the exact extent to which social learning is responsible for the maintenance of these differences remains ambiguous.

To establish beyond doubt experimentally that a particular group-typical behaviour, such as ant dipping, is underpinned by social learning, and is not the result of genetic pre-programming or ecological influences on asocial learning processes, two manipulations are necessary. Firstly, a sample of individuals from one group must be transferred to another, preferably at a formative age. Should they adopt the form of the behaviour common to their new group, genetic causes of group behavioural differences can be discounted. Next, the populations in question must be collectively removed from their respective environments and transferred to one another's former habitats. Should they continue to exhibit group-typical behaviour that is different from that of the area's former residents, environmental influences can be rejected as being responsible for asocially shaping the actions of the group's members. Social learning will then remain as

the only feasible explanation of the variation in different populations' behaviour (Laland and Hoppitt 2003).

Unfortunately, logistic and ethical considerations prevent this sort of experiment being conducted on chimpanzees (Laland and Hoppitt 2003; Whiten et al. 2007), or for that matter on most other primates; which means that if we want to find incontrovertible evidence of the existence of social information transfer resulting in group-specific behaviours in non-human animals ('culture' in its most basic sense), we must consider more distantly related species.

### **Model Species and Insights into Information Flow Through Populations**

One of the most elegant demonstrations to date of socially transmitted information determining group behaviour comes not from primates, but from fish. Using the translocation protocol described above, Helfman and Schultz (1984) were able to show that French grunts (*Haemulon flavolineatum*) – a smaller, less endangered, and much more easily moved species than chimpanzees – taken from one population and introduced to another, adopted the same schooling sites and migration routes as the already-present residents. Not only this, but control fish moved to locations from which residents had been removed, did *not* adopt the same behaviour as their former occupants. Thus, Helfman and Schultz were able to conclude that information about schooling sites and migration routes must be socially transmitted between shoal-mates, rather than being environmentally controlled or genetically encoded. Warner (1988) carried out similar experiment on Bluehead Wrasse, again finding compelling evidence that local traditions are reliant on social learning, and persist for longer than the lifetime of an individual fish. Cross-fostering experiments in birds have proven equally effective. Norton-Griffiths (1967) cross-fostered oystercatcher offspring amongst groups of birds exhibiting two different foraging techniques, finding that the birds acquired their adoptive parents' behaviour. Strikingly, Slagsvold and Wiebe (2007) cross-fostered blue tits and great tits, and once again found that young birds acquired the dietary traditions of their foster parents, even though these were different species. This is a powerful illustration of the potency of cultural transmission in nature.

Experimenting on model species in a still more controlled setting – that of the laboratory – can provide illuminating details about what factors are important in the spread of social information through populations. Boogert et al. (2006, 2008) investigated the extent to which the spread of innovations in captive groups of starlings (*Sturnus vulgaris*) could be predicted by knowledge of association patterns, social rank orders, asocial learning abilities and individuals' responses to

novel stimuli (neophobia). Each group was presented with six different novel foraging tasks, all containing mealworm ‘rewards’. Individual tasks were presented repeatedly over one to two days, and all birds’ interactions with, and solutions (defined as successful acquisition of a mealworm) to, a task were recorded. These data were then related to previously recorded measures of association, social rank, individual learning capacity and neophobia using linear models. It was found that the birds that tended to contact and solve the tasks first were those that were least hesitant to feed in the proximity of novel objects when tested in isolation, and that performed best during tests of asocial learning. They were also generally of a high competitive rank.

Boogert et al. (2008) detected a significant negative correlation between the latency of a bird contacting a task, and the length of time that elapsed before it subsequently solved the task. In other words, birds that did not begin to interact with tasks until later on in a given set of trials typically required less time to solve them than did those that approached them earlier. This was not the case in trials where the starlings were tested alone (i.e. isolated birds that took longer initially to interact with a task were no quicker at solving it once they *did* contact it, than were those that interacted with it after less of a delay). Together, these results suggested that birds that were slower to contact tasks when they were presented in a group context benefited from the opportunity to observe group-mates’ task-solving demonstrations, reducing the time they themselves needed to solve the tasks once they began interacting with them (Day 2003) – an interpretation that was substantiated when network-based diffusion analyses were later applied to the data (Hoppitt et al. 2010).

Model species can also be used in the development of new experimental and analytical techniques for detecting the social transmission of information through populations. Kendal et al. (2009b) proposed the ‘option-bias’ method as a means of inferring the occurrence of social learning during the spread of a behaviour through a group. This method relies on the premise that, once genetic and ecological factors have been accounted for, and once alternative sources of bias (chance or asocial learning) have been ruled out on probabilistic grounds, social learning should result in greater behavioural homogeneity than would otherwise be expected. If, for instance, a task can potentially be solved in several ways, but most or all of the members of a group solve it in the same way as did the original ‘innovator’, this will provide strong evidence for social learning.

In one of several tests to validate the ability of the option-bias method to detect social learning, Kendal et al. (2009a) re-analysed data gathered by Coolen et al. (2003) on a species of freshwater fish,

the nine-spined stickleback (*Pungitius pungitius*). This species is known to use social information, being sensitive to information conveyed by the actions of conspecifics, and even hetero-specifics (Coolen et al. 2003). In the particular experiment assessed by Kendal et al. (2009a), sticklebacks were allowed to observe demonstrator conspecifics feeding at two food patches of differing profitabilities. The number of visits they made to each patch over the ten minutes immediately after the demonstrators had been removed was recorded. Observer fish made significantly more visits to the 'richer' demonstrated patch than to the 'poor' patch, clear evidence for 'public information use'. Analysis using the option-bias method corroborated this, showing that nine-spined sticklebacks exhibited much more homogeneous patch choice behaviour than would be predicted by chance or asocial learning. In principle, these methods can also be applied to human data, and archaeologists and anthropologists are beginning to do so.

### ***Model Species and Social Learning 'Strategies'***

Sicklebacks are also proving to be a useful model species with which to investigate social learning 'strategies'. Evolutionary game theory and population genetic models predict that animals should not be indiscriminate with regards to when they copy others as opposed to relying on their own experience or asocial learning (Boyd and Richerson 1985; Rogers 1998; Giraldeau et al. 2002). Rather, they should exploit social information conditionally, according to evolved rules, or 'strategies' (Laland 2004).

Studies conducted on nine-spined sticklebacks strongly support these predictions. As described above, sticklebacks have been shown to be capable of 'public information use', extracting (and acting upon) information about the quality of food patches through observation of others' behaviour (Coolen et al. 2005). They also weight information by time, ignoring social cues if they have up-to-date and reliable knowledge of their own, but switching to exploiting public information if their personal information is outdated, unreliable, or altogether lacking (van Bergen et al. 2004; Coolen et al. 2005) – an example of a 'copy when uncertain' strategy. By relying preferentially on personal information, and utilizing social information selectively, nine-spines are able to avoid the potentially maladaptive informational cascades that could result from blindly copying the activity of others who may themselves not be behaving optimally (Giraldeau et al. 2002). Humans have also been shown to employ a similar strategy during computer-based tasks. McElreath et al. (2005) designed a task in which subjects could repeatedly plant one of two 'crops' of differing yields. Reliance on information from group-mates was found to increase when individual learning was manipulated to be

relatively inaccurate, confirming use of the ‘copy when uncertain’ rule. Similarly, across a range of tasks, Morgan et al. (2011) found subjects were more reliant on social information when they expressed greater uncertainty in their own ability.

Another instance of humans and sticklebacks employing functionally similar (albeit, mechanistically different) social learning strategies is in the case of a ‘copy when asocial learning is costly’ strategy. Individual learning via direct sampling of the environment, although usually accurate, can incur significant fitness costs in the form of injury, predation, and ‘missed opportunities’ (loss of time or energy that could have been spent elsewhere). Boyd and Richerson’s (1985) ‘costly information hypothesis’ proposes that animals face an evolutionary trade-off between acquiring accurate but costly ‘personal’ information, and less accurate but cheap ‘social’ information. One way in which this trade-off might be expected to manifest itself is by individuals being more inclined to exploit social information when personal information is costly. Sure enough, Coolen et al. (2003) demonstrated that nine-spined sticklebacks comply with this rule, finding that these fish prefer to shelter in vegetation (where they are presumably at less risk of predation) and base their choice of foraging patch on information gained through watching feeding conspecifics, than to sample the foraging patches for themselves before making a choice. Conversely, three-spined sticklebacks did not exhibit evidence for public information use, a finding thought to be related to their lesser vulnerability to predation (see below). In the case of humans, Morgan et al. (2011) found that individuals were more likely to copy the actions of group-mates when asocial information was manipulated to be additionally costly and when faced with a difficult (presumably time- and energy-consuming) task than when presented with an easy one, offering further evidence of the ‘copy when asocial learning is costly’ strategy in use.

Sticklebacks have also been found to employ one of three equally efficient strategies proposed by theoretical economist Karl Schlag (1998) as a means by which individuals (Schlag actually had humans in mind) might maximize their fitness in an environment where the success of others is unreliable and noisy. Schlag’s three alternatives were ‘proportional observation’, ‘proportional reservation’, and ‘proportional imitation’. In the first of these, an individual’s probability of copying others in its population is related to the payoff it perceives *them* to be receiving from whatever activity they are performing; in the second, it is related to how satisfied the individual is with *its own* payoff; and in the third, an individual’s propensity to copy is related to how much better other members of the population are doing *relative to it*. In experiments designed to test which, if any, of these strategies

nine-spined sticklebacks employed when in a ‘noisy’ environment, Pike et al. (2010) found strong evidence that fish exhibited an increasing propensity to copy demonstrators as the demonstrators’ payoffs rose (i.e. they adhered to the strategy of ‘proportional observation’). Concerning humans, Morgan et al. (2011) found evidence for ‘proportional observation’ with conditional ‘proportional imitation’.

Schlag’s analyses (1998, 1999) reveal that this simple strategy possesses ‘hill-climbing’ properties. Thus the use of this rule by these fish may plausibly enable sticklebacks to exhibit cumulative increases in the efficiency with which they exploit prey. The deployment of a behavioural rule that has a possible ‘ratcheting’ quality has hitherto not been demonstrated in any animal other than humans, and it is interesting that the first demonstration of such a rule should come not from a fellow primate, but from a species so distantly related to us as the nine-spined stickleback.

### ***Model Species and Different Social Learning Processes***

The social transmission of information from one individual to another can occur by a number of means (for comprehensive reviews of the topic, see Whiten and Ham 1992; Heyes 1994; Zentall 1996; Hoppitt and Laland 2008). Suffice to say here that there are several known mechanisms and certain forms of ‘copying’ that are widely believed to be more cognitively demanding than others. ‘Local enhancement’ (Thorpe 1963; Hoppitt and Laland 2008), for example, occurs when a ‘demonstrator’s’ interactions with objects at a particular location increase the probability of an ‘observer’ visiting or interacting with objects at that location, and is considered to be a relatively simple form of social learning. At the opposite end of the spectrum, ‘production imitation’ (Byrne 2002), which involves an observer seeing a demonstrator perform a novel act, sequence of acts, or combination of acts, and subsequently becoming more likely to perform that new act or sequence of acts, is generally thought to require quite complex cognition.

It is tempting to speculate that what may set human, and to some extent ape, cultural transmission apart from other animals, is our capacity for such cognitively complex, high-fidelity forms of social information transfer as imitation. Once again, however, evidence from experiments with model species reminds us that we must be cautious about making these assumptions. Some of the best available evidence of motor imitation in non-human animals has in fact been produced using birds. Akins and Zentall (1996) found strong evidence of body-movement copying by captive quail during ‘two-action’ tests in which birds were shown a demonstrator using either its beak or foot to depress a lever, and then allowed to interact with the lever themselves. Both pigeons (McGregor et al. 2006) and budgerigars (Dawson

and Foss 1965; Heyes and Saggesson 2002) have been shown to possess similar abilities. Furthermore, there is some indication that quail are even capable of outcome-sensitive imitation, since they are less inclined to copy their demonstrators when they observe them pecking or stepping in extinction – i.e. without reward (Akins and Zentall 1998).

### **Summary**

We advocate the use of model species in comparative studies, on three grounds. First, we have argued that the strength of homology lies in the use of multiple species, and expressed the concern that studies that limit themselves to our closest relatives may only observe a small part of the overall picture, which may be misleading. Second, we point out that model species are, by definition, amenable to experimental manipulation, and can provide rigorous and detailed information about the spread of information through populations. Finally, we have shown that studies using non-primates can yield real insights into human culture. Experimental methods and analytical techniques that are successfully developed using model organisms can later be applied to other species, including humans, in less controlled settings. The ‘option-bias’ method of Kendal et al. (2009b) is an example, being adopted for use in studies on human archaeological remains; while methods such as those used by Boogert et al. (2006, 2008) in their studies of captive starlings, could potentially be applied in the field to detect social transmission of behaviours in some of our close relatives, such as chimpanzees. We now go on to consider analogy, a second comparative approach that provides another investigative avenue and equally compelling results.

## **Non-human Animals and Functional Parallels: Insights from Non-homologous Processes**

### ***Convergent Selection for Cultural Transmission***

What studies of social learning in non-primates rapidly make clear is that there is no linear, or even continuous, accumulation of cultural transmission mechanisms across species. In fact, the opposite appears to be the case, with multiple appearances of different mechanisms and often great disparity between closely related species. For example, as detailed above, although the nine-spined stickleback shows complex cultural transmission, the closely related three-spined stickleback, despite living sympatrically to the nine-spined, possesses comparatively very simple cultural transmission and appears to be incapable of public information use (Coolen et al. 2003). Such differences between

closely related species may be the norm rather than the exception with regards to cultural transmission, and imply repeated bouts of convergent selection favouring cultural capabilities, and animal intelligence generally, as recently reported in primates (Reader et al. In Press).

This patchy distribution is manifest across different cultural transmission mechanisms, including those historically held to be cognitively complex, such as teaching (Hoppitt et al. 2008). Studies of animal teaching most commonly adopt the functional definition set out by Caro and Hauser (1992: 153), which states that:

An individual actor A can be said to teach if it modifies its behaviour only in the presence of a naive observer, B, at some cost or at least without obtaining an immediate benefit for itself. A's behaviour thereby encourages or punishes B's behaviour, or provides B with experience, or sets an example for B. As a result, B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all.

A key aspect of this definition is that it does not require the inference of any mental states in either the teacher or the pupil. Although this might seem surprising from a human perspective, where the intention to impart information is part of teaching, functional definitions are critically important to biologists as they make testable predictions due to the intense difficulty of attributing mental states to animals. It should also be noted that this definition encompasses all examples of human teaching. Perhaps more surprising, however, is that the three species in which there is currently the strongest evidence for teaching are meerkats (Thornton and McAuliffe 2006), pied babblers (Raihani and Ridley 2008) and the ant (*Temnothorax albipennis*) (Franks and Richardson 2006).

The extremely scattered distribution of cultural transmission mechanisms suggests that if we wish to piece together anything approaching a complete phylogeny we would need to perform an exhaustive investigation across a broad range of animal taxa. This endeavour would be both expensive and of debatable value. The patchy distribution instead opens up a new avenue of investigation, allowing us to consider why certain species might possess particular capabilities while others do not, and focusing not at the level of homologous mechanism but rather on analogous functionally equivalent traits.

The case of the sticklebacks provides one such opportunity, since it suggests that natural selection fashions highly specific cultural capabilities in particular species of animals, according to their ecology and life history. The three-spined and nine-spined species live sympatrically, occupying the same areas, however there must be something different in their ecologies that leads to one species and not the other

evolving the ability to use public information. During experiments on both species, Coolen et al. (2003) observed that only the nine-spined sticklebacks hid in vegetation whilst observing conspecifics. They concluded that this was to decrease the risk of predation, something that is less important for three-spined as they are protected by much larger spines and a heavily armoured torso. This is supported by evidence of predator preference for nine-spined over three-spined sticklebacks (Hoogland et al. 1957). Coolen et al. (2003) suggest that nine-spined sticklebacks evolved the ability to use public information as it avoids the risks of examining patch quality directly. The lower predation risk to three-spined sticklebacks removed this necessity and so seemingly they never required this ability. The aforementioned study implies that, while the broad capability for social learning is widespread across animals, particular species may be gifted with enhanced cultural capabilities by selection, tailored to their particular needs, in an extremely species-specific manner. Rather than expecting broad groups, such as primates, to excel at culture, we would be better placed asking which specific groups (i.e. macaques, capuchins, chimpanzees) excel. Conversely, we are likely to find that many primates (e.g. gibbons, langurs, bushbabies) are unexceptional in their cultural capabilities, and witness superior performance to these amongst non-primates.

Animal teaching provides a case in point. The seemingly bizarre taxonomic distribution of teaching has prompted discussion of what life-history traits might facilitate its evolution (Hoppitt et al. 2008). Although these examples of animal teaching are undoubtedly mechanistically dissimilar to human teaching, they are functionally equivalent and solve analogous problems. It follows that a knowledge of the selective pressures driving the evolution of teaching in animal species may shed light on the evolution of teaching in humans. Franks and Richardson (2006) examined teaching in ants, which takes the form of ‘tandem-running’, by which one individual teaches another the location of a food source such that it can then be harvested at a greater rate. To do this, the teaching ant slows its movement to a quarter of its typical speed and only proceeds when its following pupil catches up and taps it with their antennae. The pupil regularly runs in loops behind the teacher, identifying landmarks to aid in successful recall of the route later. Although this process impacts upon the teachers collecting efficiency, it increases the chance of others finding the food source and thereby aids the colony. Not all ant species, however, show tandem-running, others instead use the scent trails left by other individuals to locate food sources. By comparing colonies it was found that tandem-running occurs in those with smaller populations. Franks and Richardson (*ibid.*) argued that in these smaller

groups information on food location is more likely to be lost when using just scent trails and this creates a pressure to actively pass knowledge between individuals leading to the evolution of teaching. This is confirmed by another study (Beekman et al. 2001) that found that ants were only able to use scent trails to forage effectively when their colony was over a critical size.

In the case of teaching, comparisons between dissimilar, but closely related species (as with the ants) are supplemented by studies looking for common features across the species that show teaching. From this perspective it has been argued that teaching should be viewed as a special case of cooperation (Thornton and Raihani 2008) and should therefore obey Hamilton's Rule, which states that cooperation will occur if the cost to the teacher is less than the benefit to the pupil, scaled by the relatedness between the two individuals. By this account, teaching should be more likely to appear where naïve individuals cannot easily acquire information or skills without the aid of a teacher. This is illustrated with teaching in meerkats, whereby adults educate young in the process of successfully catching and killing dangerous scorpions (Thornton and McAuliffe 2006). This is achieved by the adults catching scorpions for the young and bringing them first dead, then alive but stingless, and finally unaltered. Youngsters progress through these stages as they age, and the adults gauge the age of the young by the calls they make. Meerkats taught in this way show much better performance when catching scorpions for themselves. The danger posed by catching potentially lethal prey creates a problem of sufficient difficulty that the benefits of modifying prey to help youngsters learn outweighs the cost of the teacher having to sacrifice caught prey, even when the degree of relatedness between the two individuals is taken into account. These findings are backed up by theoretical analyses, which found that the evolution of teaching critically depends on both the degree of problem difficulty and the relatedness between individuals (Fogarty et al. 2011). The rare incidents of animal teaching appear disproportionately to occur amongst cooperative breeding species (Hoppitt et al. 2008). This may be no coincidence, since cooperative breeders frequently exhibit close relatedness amongst tutor and pupil, and multiple tutors share the burden of teaching, reducing its per capita cost. As humans too have been characterized as cooperative breeders (Hrdy 1999), conceivably this was a critical factor leading to the appearance of teaching in humans, uniquely amongst the apes.

In summary, teaching, widely assumed to require complex cognitive ability, appears in a diverse array of species not otherwise known for complex intelligence. Its otherwise conspicuous absence from our closest relatives can be explained, however, through consideration of

relevant ecological and life-history factors. This suggests that such processes are not necessarily cognitive achievements, but are better viewed as solutions to particular problems faced by a subset of species. It is, in fact, the scarcity of conditions where a cost–benefit analysis favours investment in costly cultural transmission processes that dictates the rarity of the mechanism and creates the patchy distribution we observe.

### ***Human Convergence***

What does this imply for human culture? Were our ancestors merely in the right place at the right time, as it were, to face the environmental conditions necessary for the evolution of human-level culture? Furthermore, if cultural transmission can apparently be divorced from cognitive complexity, then why are humans both the most cognitively and culturally complex species on earth? We suspect that the answer to this lies in the peculiarities of human culture and cultural transmission, which is indeed distinct from that of the other animals discussed before in that it shows a high level of fidelity in information transfer (Tomasello 1994). Just as nine-spined sticklebacks were distinct from three-spined sticklebacks in that they could use cultural transmission to determine not only food location but also quality, humans are distinct from other apes in their ability to transfer information with very high fidelity across numerous generations. This is most apparent in the steady elaboration of behaviour and ideas to create improvements to existing technology – the ‘ratchet effect’. This cumulative culture is typically illustrated with the progression from early stone hammering tools, through hand-held hafted hammers with metal heads, through to nineteenth-century steam hammers and twentieth-century electric hammers, though its impact is ubiquitous across human culture.

Perhaps then, if we are interested in human culture, we should focus our attention on the processes that underlie cumulative culture. It might appear that cumulative culture is as unique as human-level culture, with isolated reports of cumulative culture in wild chimpanzees (Boesch 2003) failing to be backed by experimental studies (Marshall-Pescini and Whiten 2008). However, if we broaden our scope beyond primates we again encounter species that show greater similarity to us than our nearest relatives. Evidence for cumulative culture has been suggested in cetaceans, the group comprising whales and dolphins. The appearance in humpback whales of ‘lobtail’ feeding, an elaboration of ‘bubble-cloud’ feeding that allowed greater use of a pre-existing food source, has been argued as suggestive of cumulative modification (Rendell and Whitehead 2001). However, the best evidence, outside of humans, probably comes from the corvids,

a group of birds comprising crows, ravens and jays, among others. New Caledonian crows are known tool users (Hunt 1995) and use tools cut from the leaves of the *Pandanus* plant in extractive foraging. Cumulative culture has been argued in the design of these leaf tools (Hunt and Gray 2003), with three designs known across the island inhabited by the species that show continuous and overlapping ranges. The lack of an environmental correlate and the similarity in the manufacture of the three designs is highly suggestive of a single origin of leaf-tool manufacture that later elaborated and diversified through a cumulative process.

If we apply a similar logic to before, the similarities between apes and corvids should reveal insights into why these species show cultural transmission processes that allow the cumulative modification of culturally transmitted information. Although having separated over 300 million years ago and being morphologically very dissimilar, both corvids and apes show a remarkable cognitive similarity that has led some to describe corvids as ‘feathered apes’ (Emery 2004; Emery and Clayton 2004). As well as tool use, both groups are thought to show complex physical cognition (Seed et al. 2006; Mulcahy and Call 2006), episodic-like memory (Clayton et al. 2007) and are also capable of transitive inference, the ability to infer that if  $A > B$  and  $B > C$ , then  $A > C$  (Paz-y-miño et al. 2004), an ability which has also been found in cichlid fish (Grosenick et al. 2007). Corvids are also capable of mirror self-recognition (Gallup 1970; Prior et al. 2008) and show at least as much evidence as chimpanzees for theory of mind – the ability to understand that other individuals have goals and beliefs that are distinct from your own and may be false (Clayton et al. 2007) – although others would argue that this amounts to no evidence at all (Penn and Povinelli 2007). Thus it seems that the similarities between corvids and apes add up to a complex general intelligence of which cumulative cultural transmission, if present, is only a part. If we wish to understand why we have cumulative culture, we must also ask why we have an enhanced intellect more generally.

Unsurprisingly, the evolution of intelligence has received a great amount of attention, although it is still far from resolution. An influential theory is that of the social intelligence hypothesis, the notion that intelligence evolved in order to deal with the problems associated with group living (Humphrey 1976). This continues to receive attention today (Dunbar 2003; Bond et al. 2003). However, although there is much support, it is also clear that the social intelligence hypothesis alone cannot explain the evolution of intelligence (Holekamp 2006). Hyaenas, for example, although socially as complex as many primates, possess a much lesser intelligence, which cannot be accounted for by the social intelligence hypothesis (*ibid.*). Seed et al.

(2009) reasoned that as both apes and corvids show increased intelligence then shared environmental and life-history traits would provide evidence as to the driving force behind their cognitive abilities. Their review of six of the most commonly raised hypotheses found that all were applicable to corvids as well as primates. Both groups, for example, feed on spatiotemporally dispersed resources. Apes show an increased reliance on tropical plant foods, because as there are no seasons in the tropics each species fruits at a different time of year. To forage effectively apes need to keep track of both the location of plants of different species and also to know when fruit will be available from them. Similarly, many corvids cache food, burying items for later consumption. Experiments have shown that not only are corvids highly efficient at remembering the location of food caches, they also take into account the perishability of food items and so know when to return to them (Clayton and Dickinson 1998) – this provides a spatiotemporally dispersed food source, just as faced by apes. Seed et al. (2009) examined other ‘physical’ factors and found that omnivory, extractive foraging, complex foraging and tool use were common to both groups. They then considered ‘social’ factors and found that, again, both groups showed Machiavellian behavioural strategies, cooperation, coordination and complex cultural transmission. Although it may be tempting, from the perspective of this chapter, to place emphasis on the final shared factor – complex cultural transmission – this would be exceedingly premature. The common ground between the two groups adds up to a suite of complex challenges and behaviours to match them, of which cultural transmission is only one. Currently all these factors seem equally implicated in the origins of a complex intelligence capable of generating human culture.

## Conclusion

It is through the two routes of homology and analogy that non-primate animals are able to increase our understanding of cultural transmission. The use of non-primate model organisms, selected for their suitability to experimentation, provides an amenable, powerful and cost-effective method to investigate cultural transmission processes. These species also allow the development of powerful statistical tools that can, and are, being used in studies of cultural transmission in other species, including humans. Furthermore, work with model organisms, even if not conducted with the specific view to answering human-related questions, is of use in broadening our general understanding of social learning processes, and in increasing our appreciation of the capabilities of animals that may be only very distantly

related to us. The use of analogy in addition to homology through comparisons between species, either close relatives that show disparity, or distant relatives that show convergence, allows investigation of the different factors that drive the evolution of cultural transmission processes. The role of these studies in understanding the evolution of human cultural transmission does not rely on common mechanisms, as they represent separately derived solutions to the same problems. Whilst such comparisons suggest that many mechanisms, including teaching, need not be cognitively complex and are best considered within an evolutionary cost–benefit framework, they also reveal that human cultural transmission and cumulative culture seem tied in with an overall complex intellect. Thus, whilst work carried out with non-primates both reinforces and refines the uniqueness of human cultural transmission, it also reveals the wealth of information that non-primates offer and the necessity of their study if we are to gain a complete understanding of culture.

## Acknowledgements

Research supported in part by an ERC Advanced Grant to KNL (EVOCULTURE 232823).

## References

- Akins, C.K. and T.R. Zentall. 1996. 'Imitative Learning in Male Japanese Quail Using the Two-action Method', *Journal of Comparative Psychology* 110: 316–20.
- \_\_\_\_\_, and T.R. Zentall. 1998. 'Imitation in Japanese Quail: The Role of Demonstrator Reinforcement', *Psychonomic Bulletin and Review* 5: 694–97.
- Beekman, M., D. Sumpter and F. Ratnieks. 2001. 'Phase Transition Between Disordered and Ordered Foraging in Pharaoh's Ants', *Proceedings of the National Academy of Sciences* 98: 9703–6.
- Bergen, Y. van, J. Coolen and K.N. Laland. 2004. 'Nine-spined Sticklebacks Exploit the Most Reliable Source when Public and Private Information Conflict', *Proceedings of the Royal Society of London B* 271: 957–62.
- Boesch, C. 2003. 'Is Culture a Golden Barrier between Human and Chimpanzee?', *Evolutionary Anthropology* 12: 82–91.
- \_\_\_\_\_, and H. Boesch. 1990. 'Tool Use and Tool Making in Wild Chimpanzees', *Folia Primatologica* 54: 86–99.
- Bond, A.B., A.C. Kamil and R.P. Balda. 2003. 'Social Complexity and Transitive Inference in Corvids', *Animal Behaviour* 65: 479–87.

- Boogert, N.J., S.M. Reader, W. Hoppitt and K.N. Laland. 2008. 'The Origin and Spread of Innovation in Starlings', *Animal Behaviour* 75: 1509–18.
- \_\_\_\_\_. 2006. 'The Relation between Social Rank, Neophobia and Individual Learning in Starlings', *Animal Behaviour* 72: 1229–39.
- Boyd, R. and P.J. Richerson. 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.
- Byrne, R.W. 2002. 'Imitation of Novel Complex Actions: What Does the Evidence from Animals Mean?', *Advances in the Study of Behavior* 31: 31–77.
- Caro, T.M. and M.D. Hauser. 1992. 'Is There Teaching in Nonhuman Animals?', *The Quarterly Review of Biology* 67: 151–74.
- Clayton, N.S., J.M. Dally and N.J. Emery. 2007. 'Social Cognition by Food-catching Corvids: The Western Scrub Jay as a Natural Psychologist', *Philosophical Transactions of the Royal Society of London, Series B* 362: 507–22.
- \_\_\_\_\_. 1998. 'Episodic-like Memory during Cache Recovery by Scrub Jays', *Nature* 395: 272–74.
- Clutton-Brock, T.H. and P.H. Harvey. 1984. 'Comparative Approaches to Investigating Adaption', in J.R. Krebs and N.B. Davies (eds), *Behavioural Ecology*. Oxford: Blackwell, pp. 7–29.
- Coolen, I., Y. van Bergen, R.L. Day and K.N. Laland. 2003. 'Species Difference in Adaptive Use of Public Information in Sticklebacks', *Proceedings of the Royal Society of London B* 270: 2413–19.
- \_\_\_\_\_. 2005. A.J.W. Ward, P.I.B. Hart and K.N. Laland. 2005. 'Foraging Nine-spined Sticklebacks Prefer to Rely on Public Information over Simpler Social Cues', *Behavioral Ecology* 16: 865–70.
- Cullen, E. 1957. 'Adaptations in the Kittiwake to Cliff-nesting', *Ibis* 99: 275–302.
- Dawson, B.V. and B.M. Foss. 1965. 'Observational Learning in Budgerigars', *Animal Behaviour* 13: 470–74.
- Day, R.L. 2003. 'Innovation and Social Learning in Monkeys and Fish: Empirical Findings and their Application to Reintroduction Techniques', Ph.D. thesis, University of Cambridge.
- Dunbar, R.I.M. 1995. 'Neocortex Size and Group Size in Primates: A Test of the Hypothesis', *Journal of Human Evolution* 28: 287–96.
- \_\_\_\_\_. 2003. 'The Social Brain: Mind, Language, and Society in Evolutionary Perspective', *Annual Review of Anthropology* 32: 163–81.
- \_\_\_\_\_. 1998. and J. Bever. 1998. 'Neocortex Size Predicts Group Size in Carnivores and Some Insectivores', *Ethology* 104: 695–708.
- Durham, W.H. 1991. *Co-evolution: Genes, Culture and Human Diversity*. Stanford: Stanford University Press.
- Emery, N.J. 2004. 'Are Corvids "Feathered Apes"? Cognitive Evolution in Crows, Jays, Rooks and Jackdaws', in S. Watanabe (ed.) *Comparative Analysis of Minds*. Tokyo: Keio University Press, pp. 181–213.
- \_\_\_\_\_. 2004. and N.S. Clayton. 2004. 'The Mentality of Crows: Convergent Evolution of Intelligence in Corvids and Apes', *Science* 306: 1903–7.

- Fields, S. and M. Johnston. 2005. 'Cell Biology: Whither Model Organism Research?', *Science* 307: 1885–86.
- Franks, N.R. and T. Richardson. 2006. 'Teaching in Tandem-running Ants', *Nature* 439: 153.
- Gallup, G.G. 1970. 'Chimpanzees: Self-recognition', *Science* 167: 86–87.
- Giraldeau, L.A., T.J. Valone and J.J. Templeton. 2002. 'Potential Disadvantages of Using Socially Acquired Information', *Philosophical Transactions of the Royal Society of London, Series B* 357: 1559–66.
- Grosenick, L., T. Clement and R. Fernald. 2007. 'Fish can Infer Social Rank by Observation Alone', *Nature* 445: 429–32.
- Fogarty, L., P. Strimling, and K.N. Laland. 2011. 'The Evolution of Teaching', *Evolution* 65(10): 2760–70.
- Harvey, P.H. and M.D. Pagel. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Helfman, G.S. and E.T. Schultz. 1984. 'Social Tradition of Behavioural Traditions in a Coral Reef Fish', *Animal Behaviour* 32: 379–84.
- Heyes, C.M. 1994. 'Social Learning in Animals: Categories and Mechanisms', *Biological Reviews* 69: 207–31.
- \_\_\_\_\_ and B.G. Galef Jr. (eds). 1996. *Social Learning and the Roots of Culture*. New York: Academic Press.
- \_\_\_\_\_ and A. Saggerson. 2002. 'Testing for Imitative and Non-imitative Social Learning in the Budgerigar Using a Two-object/Two-action Test', *Animal Behaviour* 64: 851–59.
- Holekamp, K.E. 2006. 'Questioning the Social Intelligence Hypothesis', *Trends in Cognitive Sciences* 11: 65–69.
- Hoogland, R., D. Morris and N. Tinbergen. 1957. 'The Spines of Sticklebacks (*Gasterosteus* and *Pygosteus*) as Means of Defence against Predators (*Pera* and *Esox*)', *Behaviour* 10: 205–37.
- Hopper, L.M., A. Spiteri, S.P. Lambeth, S.J. Schapiro, V. Horner and A. Whiten. 2007. 'Experimental Studies of Traditions and Underlying Transmission Processes in Chimpanzees', *Animal Behaviour* 73: 1021–302.
- Hoppitt, W., N.J. Boogert and K.N. Laland. 2010. 'Detecting Social Transmission in Networks', *Journal of Theoretical Biology* 263: 544–55.
- \_\_\_\_\_ .G. Brown, R.L. Kendal, L. Rendell, A. Thornton, M. Webster and K.N. Laland. 2008. 'Lessons from Animal Teaching', *Trends in Ecology and Evolution* 23: 486–93.
- \_\_\_\_\_ and K.N. Laland. 2008. 'Social Processes Influencing Learning in Animals: A Review of the Evidence', *Advances in the Study of Behaviour* 38: 105–65.
- Horner, V. and F.B.M. de Waal. 2009. 'Controlled Studies of Chimpanzee Cultural Transmission', *Progress in Brain Research* 178: 3–15.
- Hrdy, S.B. 1999. *Mother Nature: Maternal Instincts and How They Shape the Human Species*. London: Chatto and Windus.
- Humle, T. and T. Matsuzawa. 2002. 'Ant Dipping among the Chimpanzees of Bossou, Guinea, and Some Comparisons with Other Sites', *American Journal of Primatology* 58: 133–48.

- Humphrey, N.K. 1976. 'The Social Function of Intellect', in P.P.G. Bateson and R.A. Hinde (eds) *Growing Points in Ethology*. Cambridge: Cambridge University Press, pp. 303–17.
- Hunt, G.R. 1995. 'Manufacture and Use of Hook-tools by New Caledonian Crows', *Nature* 379: 249–51.
- \_\_\_\_\_ and R.D. Gray. 2003. 'Diversification and Cumulative Evolution in New Caledonian Crow Tool Manufacture', *Proceedings of the Royal Society B* 270: 867–74.
- Jones, E.A. 2005. 'Xenopus: A Prince among Models for Pronephric Kidney Development', *Journal of the American Society of Nephrology* 16: 313–21.
- Kendal, J., L. Rendell, T.W. Pike and K.N. Laland. 2009a. 'Nine-spined Sticklebacks Deploy a Hill-climbing Social Learning Strategy', *Behavioral Ecology* 20: 238–44.
- Kendal, R.L., J.R. Kendal, W. Hoppitt and K.N. Laland. 2009b. 'Identifying Social Learning in Animal Populations: A New 'Option-bias' Method', *PLoS One* 4: 1–9.
- Kroeber, A.L. and C. Kluckholm. 1952. 'Culture: A Critical Review of the Concepts and Definitions', *Papers of the Peabody Museum of American Archaeology and Ethnology* 47: 1–223.
- Laland, K.N. 2004. 'Social Learning Strategies', *Learning and Behavior* 32: 4–14.
- \_\_\_\_\_ and B.G. Galef Jr. (eds). 2009. *The Question of Animal Culture*. Cambridge, MA: Harvard University Press.
- \_\_\_\_\_ and W.J.E. Hoppitt. 2003. 'Do Animals Have Culture?', *Evolutionary Anthropology* 12: 150–59.
- \_\_\_\_\_ and V. Janik. 2006. 'The Animal Cultures Debate', *Trends in Ecology and Evolution* 21: 542–47.
- Lefebvre, L., S.M. Reader and D. Sol. 2004. 'Brains, Innovations and Evolution in Birds and Primates', *Brain Behaviour and Evolution* 63: 233–46.
- Lovejoy, C.O. 2009. 'Reexamining Human Origins in Light of *Ardipithecus ramidus*', *Science* 326: 74.
- Marshall-Pescini, S. and A. Whiten. 2008. 'Chimpanzees (*Pan Troglodytes*) and the Question of Cumulative Culture: An Experimental Approach', *Animal Cognition* 11: 449–56.
- McElreath, R., M. Lubell, P.J. Richerson, T. Waring, W. Baum and E. Edsten. 2005. 'Applying Evolutionary Models to the Laboratory Study of Social Learning', *Evolution and Human Behavior* 26: 483–508.
- McGregor, A., A. Saggerson, J. Pearce and C. Heyes. 2006. 'Blind Imitation in Pigeons, *Columba livia*', *Animal Behaviour* 72: 287–96.
- McGrew, W.C. 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge: Cambridge University Press.
- Mobius, Y., C. Boesch, K. Koops, T. Matsuzawa and T. Humle. 2008. 'Cultural Differences in Army Ant Predation by West African Chimpanzees? A Comparative Study of Microecological Variables', *Animal Behaviour* 76: 37–45.

- Morgan, T., L. Rendell, M. Ehn, W. Hoppitt and K. Laland. 2011. 'The Evolutionary Basis of Human Social Learning', *Proceedings of the Royal Society B* 279: 653–62.
- Mulcahy, N.J. and J. Call. 2006. 'How Great Apes Perform on a Modified Trap-tube Test', *Animal Cognition* 9: 193–99.
- Norton-Griffiths, M.N. 1967. 'Some Ecological Aspects of the Feeding Behaviour of the Oystercatcher *Haematopus ostralegus* on the Edible Mussel *Mytilus edulis*', *Ibis* 109: 412–24.
- Paz-y-miño, G., A.B. Bond, A.C. Kamil and R.P. Balda. 2004. 'Pinyon Jays use Transitive Inference to Predict Social Dominance', *Nature* 430: 778–81.
- Penn, D.C. and D.J. Povinelli. 2007. 'On the Lack of Evidence that Non-human Animals Possess Anything Remotely Resembling a "Theory of Mind"', *Philosophical Transactions of the Royal Society of London, Series B* 362: 731–44.
- Pike, T.W., J.R. Kendal, L.E. Rendell and K.N. Laland. 2010. 'Learning by Proportional Observation in a Species of Fish', *Behavioral Ecology* 21: 570–75.
- Plotkin, H. 1997. *Evolution in Mind: An Introduction to Evolutionary Psychology*. London: Allen Lane.
- Prior, H., A. Schwarz and O. Gunturkun. 2008. 'Mirror-induced Behavior in the Magpie (*Pica Pica*): Evidence of Self Recognition', *PloS Biology* 6: e202.
- Raihani, N.J. and A.R. Ridley. 2008. 'Experimental Evidence for Teaching in Wild Pied Babblers', *Animal Behaviour* 75: 3–11.
- Reader, S.M., Y. Hager and K.N. Laland. In Press. 'The Evolution of Primate General Intelligence', *Philosophical Transactions of the Royal Society of London, Series B*.
- Rendell, L. and H. Whitehead. 2001. 'Culture in Whales and Dolphins', *Behavioral and Brain Sciences* 24: 309–82.
- Rogers, A.R. 1998. 'Does Biology Constrain Culture?', *American Anthropologist* 90: 819–31.
- Schlag, K. 1998. 'Why Imitate, and if so, How?', *Journal of Economic Theory* 78: 130–56.
- \_\_\_\_\_. 1999. 'Which One Should I Imitate?', *Journal of Mathematical Economics* 31: 493–522.
- Seed, A.M., N.J. Emery and N.S. Clayton. 2009. 'Intelligence in Corvids and Apes: A Case of Convergent Evolution?', *Ethology* 115: 401–20.
- \_\_\_\_\_. S. Tebbich, N.J. Emery and N.S. Clayton. 2006. 'Investigating Physical Cognition in Rooks (*Corvus Frugilegus*)', *Current Biology* 16: 697–701.
- Shultz, S. and R.I.M. Dunbar. 2006. 'Both Social and Ecological Factors Predict Ungulate Brain Size', *Proceedings of the Royal Society B* 273: 207–15.
- Slagsvold, T. and K.L. Wiebe. 2007. 'Learning the Ecological Niche', *Proceedings of the Royal Society B* 274: 19–23.
- Thornton, A. and K. McAuliffe. 2006. 'Teaching in Wild Meerkats', *Science* 313: 227–29.

- \_\_\_\_ and N.J. Raihani. 2008. 'The Evolution of Teaching', *Animal Behaviour* 75: 1823–36.
- Thorpe, W. H. 1963. *Learning and Instinct in Animals* (2nd ed.). London: Methuen.
- Tinbergen, N. 1963. 'On Aims and Methods in Ethology', *Zeitschrift für Tierpsychologie* 20: 410–33.
- \_\_\_\_\_.G.J. Broekhuisen, F. Feekees, J.C.W. Houghton, H. Kruuk and E. Szulc. 1962. 'Egg Shell Removal by the Black-headed Gull, *Larus ridibundus* L.: A Behaviour Component of Camouflage', *Behaviour* 19: 74–117.
- Tomasello, M. 1994. 'The Question of Chimpanzee Culture', in R. Wrangham, W.C. McGrew, F. de Wall and P. Heltne (eds) *Chimpanzee Cultures*. Harvard: Harvard University Press, pp. 301–17.
- Warner, R.R. 1988. 'Traditionality of Mating Site Preferences in a Coral Reef Fish', *Nature* 335: 719–21.
- Whiten, A. and D.M. Custance. 1996. 'Studies of Imitation in Chimpanzees and Children', in B.G. Galef Jr. and C.M. Heyes (eds) *Social Learning in Animals: The Roots of Culture*. New York: Academic Press, pp. 291–318.
- \_\_\_\_\_.J. Goodall, W.C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C.E.G. Tutin, R.W. Wrangham and C. Boesch. 1999. 'Cultures in Chimpanzees', *Nature* 399: 682–85.
- \_\_\_\_\_. and R. Ham. 1992. 'On the Nature and Evolution of Imitation in the Animal Kingdom: Reappraisal of a Century of Research', *Advances in the Study of Behavior* 21: 239–83.
- \_\_\_\_\_.V. Horner and S. Marshall-Pescini. 2003. 'Cultural Panthropology', *Evolutionary Anthropology* 12: 92–105.
- \_\_\_\_\_.A. Spiteri, V. Horner, K.E. Bonnie, S.P. Lambeth, S.J. Schapiro and F. de Waal. 2007. 'Transmission of Multiple Traditions within and between Chimpanzee Groups', *Current Biology* 17: 1038–43.
- Zentall, T.R. 1996. 'An Analysis of Imitative Learning in Animals', in C.M. Heyes and B.G. Galef Jr. (eds) *Social Learning in Animals: The Roots of Culture*. New York: Academic Press, pp. 221–34.