Durham Research Online

Deposited in DRO:

04 August 2014

Version of attached file:

Accepted Version

Peer-review status of attached file:

Peer-reviewed

Citation for published item:

Dean, L. and Vale, G.L. and Laland, K.N. and Flynn, E.G. and Kendal, R.L. (2014) 'Human cumulative culture : a comparative perspective.', Biological reviews., 89 (2). pp. 284-301.

Further information on publisher's website:

http://dx.doi.org/10.1111/brv.12053

Publisher's copyright statement:

This is the peer reviewed version of the following article: Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E. and Kendal, R. L. (2014), Human cumulative culture: a comparative perspective. Biological Reviews, 89 (2): 284–301, which has been published in final form at http://dx.doi.org/10.1111/brv.12053. This article may be used for non-commercial purposes in accordance With Wiley Terms and Conditions for self-archiving.

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a link is made to the metadata record in DRO
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the full DRO policy for further details.

Durham University Library, Stockton Road, Durham DH1 3LY, United Kingdom
Tel : +44 (0)191 334 3042 | Fax : +44 (0)191 334 2971
https://dro.dur.ac.uk

HUMAN CUMULATIVE CULTURE: A COMPARATIVE PERSPECTIVE

Lewis G. Dean[1§*], Gill L. Vale[2§*], Kevin N. Laland[1], Emma Flynn[3] and Rachel L. Kendal[2*]

[1]Centre for Social Learning and Cognitive Evolution, School of Biology, University of St. Andrews, St. Andrews, Queen's Terrace, St. Andrews, Fife. KY16 9TS
[2]Centre for Coevolution of Biology & Culture, Department of Anthropology, Durham University, Dawson Building, Mount Joy Site, Durham. DH1 3LE
[3] Centre for Coevolution of Biology & Culture, Department of Psychology, Durham University, Mount Joy Site, Durham. DH1 3LE

*To whom correspondence should be addressed: lewis.g.dean@gmail.com, g.l.vale@durham.ac.uk, rachel.kendal@durham.ac.uk

§Both authors contributed equally to this paper.

12,228 words, including an abstract of 173 words & 1 table & 1 figure

28th April 2013

ABSTRACT

Many animals exhibit social learning and behavioural traditions, but human culture exhibits unparalleled complexity and diversity, and is unambiguously cumulative in character. These similarities and differences have spawned a debate over whether animal traditions and human culture are reliant on homologous or analogous psychological processes. Human cumulative culture combines high-fidelity transmission of cultural knowledge with beneficial modifications to generate a 'ratcheting' in technological complexity, leading to the development of traits far more complex than one individual could invent alone. Claims have been made for cumulative culture in several species of animals, including chimpanzees, orang-utans and New Caledonian crows, but these remain contentious. Whilst initial work on the topic of cumulative culture was largely theoretical, employing mathematical methods developed by population biologists, in recent years researchers from a wide range of disciplines, including psychology, biology, economics, biological anthropology, linguistics and archaeology, have turned their attention to the experimental investigation of cumulative culture. We review this literature, highlighting advances made in understanding the underlying process of cumulative culture and emphasizing areas of agreement and disagreement amongst investigators in separate fields.

Keywords: cumulative culture; cultural evolution; ratcheting; social learning; animal traditions.

I. HOW IS CULTURE 'CUMULATIVE'?

On 20th July 1969 Neil Armstrong spoke the immortal words, "That's one small step for man, one giant leap for mankind". Landing the Eagle lunar module on the moon was a huge achievement for humanity, but it was one that resulted from a series of many small steps. This crowning achievement of human endeavour was not planned and devised by Armstrong alone, but by a huge team, deploying ballistics, electronics, materials science and radio communication technologies reliant on theoretical and experimental research carried out over several centuries. Whilst the achievement of individual scientists and engineers may be ground-breaking, technological progress virtually always depends upon the work that goes before it.

The focus of this review is cumulative culture, the ability of humans to ratchet up the complexity of cultural traits over time. The example of the Apollo mission demonstrates that humans are able to increase the complexity of their technology and knowledge over many episodes of social transmission, by building on the developments of their predecessors. This ratcheting up in the complexity of cultural traits, frequently across multiple generations, has been proposed to be the hallmark of human culture (Richerson & Boyd, 2005; Enquist & Ghirlanda; Mesoudi, 2011a), but the cognitive and social processes upon which it relies remain poorly understood. Here a comparative perspective is potentially informative. While claims have been made that certain animals possess cumulative culture in rudimentary form, these are disputed and the human capacity for cumulative culture is clearly unparalleled in the animal kingdom. The question of what underlies this difference in human and animal cultures was featured in *Science* magazine's (2005) list of 100 things we don't know that we need to, as the answer to this question has far reaching implications for how we view our place in nature.

In this paper we review the current theoretical and empirical evidence addressing cumulative culture in both human and non-human animals. In doing so, we explore how human culture differs from non-human culture, before turning to the potential social and cognitive processes that may hold the key to our species' unique cumulative cultural capability.

II. CULTURE IN ANIMALS.

(1) Defining culture.

The term 'culture' is used by researchers from a broad range of disciplines, including biology, psychology, archaeology, social and biological anthropology, with each discipline drawing on different epistemological and ontological assumptions. As Sterelny (2009) points out, these different definitions of culture are not stipulative, they are hypothesis choosing. Thus, through formulating a definition, researchers have determined their focus, thereby limiting both what is investigated and how it is investigated. Using different definitions, the focus of the study of culture can cover over 11,000 species (Lumsden & Wilson, 1981) or be restricted to humans (Kroeber & Kluckhorn, 1952). The definitions ascribed to culture can impose constraints on which learning processes are deemed to underlie culture (e.g. "Culture is information capable of affecting individuals' phenotypes, which they acquire from other conspecifics by teaching or imitation", (Boyd & Richerson, 1985, page 33). Moreover, the definition also dictates whether culture is treated as the physical expression of specific behaviour patterns (van Schaik et al., 2003) or as the ideas and beliefs which lie behind behaviour patterns (D'Andrade, 2008).

Here, our primary agenda is to compare the cultural capabilities of humans and other animals, and accordingly we adopt a definition that lends itself to this objective. Following Laland and Hoppitt (2003), we define culture as "group typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information" (p. 151). This established, we now consider what is known about culture in non-human animals.

(2) The animal cultures debate.

Alongside the alternative definitions that different researchers apply to culture, there are also disagreements about the quality of the evidence necessary for a given species to be deemed 'cultural' (Galef, 1992; Laland & Hoppitt, 2003; Laland & Galef, 2009). For instance, Lefebvre and Palameta (1988) summarise nearly 100 reports of traditional behavioural patterns in animal species, including mammals, birds and fish, suggesting that animal traditions are taxonomically widespread. Although these authors did not classify these phenomena as 'culture', to the extent that the observation of a tradition can be regarded as evidence for social transmission, these species are potentially candidates for animal culture. However, it is difficult to establish unequivocally that social transmission underlies natural diffusions and inter-population behavioural variation, since individual animals might independently have been shaped by ecological conditions to perform the focal behaviour. For this reason, some researchers seek additional evidence that natural traditions are socially transmitted, for instance, relying on translocation experiments or careful analyses of the development of the behaviour. In reviewing field experiments, Reader and Biro (2010) concluded that social learning has been unequivocally demonstrated in 20 different species in the wild, including in honeybees, birds and mammals, and across a range of contexts, including foraging, predator avoidance and habitat choice. Whilst these experiments do not necessarily test whether the behaviour patterns are group typical, they do establish that the relevant information is socially transmitted. However, given that many hundreds of species of animals have been shown to be capable of social learning through experiments in captivity, this list almost certainly substantially underestimates the extent of natural animal tradition.

Primatologists Whiten and van Schaik (2007) restrict culture to those species with traditions in at least two different behavioural domains, specifically chimpanzees (*Pan troglodytes*), orangutans (*Pongo ssp*) and white-faced capuchin monkeys (*Cebus capucinus*). Whiten et al. (1999) gathered data from seven long-term chimpanzee field sites providing evidence for 39 behaviour patterns judged to be cultural by field workers, including food-processing techniques, such as nut-cracking, methods of parasite inspection and social customs, such as hand-clasp grooming. Likewise, orangutans have been proposed to show 24 social and foraging traits (van Schaik et al., 2003), while foraging traditions have been documented in white-faced capuchins (Panger et al., 2002), as have social games (Perry et al., 2003- detailed in section IV.3.b). Thus, although Whiten and van Schaik (2007) argue that culture is not unique to humans, they argue that there is only evidence of culture in primates.

These claims have been criticised by other researchers concerned that the reports of culture in primates are based upon purely observational studies, with no experimental evidence that the behavioural variation is indeed a result of socially transmitted information and not some other factor (Galef, 1992; Tomasello, 1994; Laland & Hoppitt, 2003). While such experimental procedures are available (e.g. manipulations in which individuals are experimentally transferred between populations, or populations are transferred between sites), and have been applied to some fish species (Helfman & Schultz, 1984; Warner, 1988), they are not feasible for primates. More recently, less disruptive methods have been developed for identifying social learning in the field (Laland et al., 2009; Kendal et al., 2010b).

These examples illustrate that even amongst researchers who argue that animals have culture, there is disagreement on how widespread culture is. As these arguments are fully expanded elsewhere (e.g. Laland & Galef, 2009), we turn to the specific focus of this review, that of cumulative culture.

III. CUMULATIVE CULTURE.

The idea of cumulative culture is integral to the work of cultural evolutionists (Cavalli-Sforza & Feldman, 1981; Lumsden & Wilson, 1981; Boyd & Richerson, 1985), who have developed mathematical models, based on those used in evolutionary biology, to examine how cultural innovations are introduced and spread within a population. Whilst this work was primarily focussed on culture in humans, other researchers have been interested in a comparative approach to culture. In 1994 comparative psychologist Michael Tomasello first coined a metaphor commonly used to illustrate cumulative culture, that of the 'ratchet'

(Tomasello, 1994). Tomasello argued that loss of a cultural trait across generations is prevented by high-fidelity information transmission conferred by accurate social learning processes, creating the opportunity for modifications of the cultural trait to be devised, ratcheting up its complexity or efficiency. Over time, repeated modifications result in cultural traits that are too complex to have been invented by a single individual (Tomasello et al., 1993; Tomasello, 1994; Tomasello, 1999). Several researchers have argued that this cultural 'ratchet' is a unique feature of human culture (Heyes, 1993; Tomasello et al., 1993; Tomasello, 1994; Boyd & Richerson, 1996). Theoretical analyses provide support for the link between high-fidelity transmission mechanisms and cumulative culture: irrespective of the rate of innovation, cumulative culture cannot emerge without accurate transmission (Lewis & Laland, In Press). Pradham et al (2012) have suggested that increased sociability, thus an increase in social learning opportunity, may be sufficient for cumulative culture to occur, although some researchers argue that high fidelity transmission is not present in non-humans (Tennie et al., 2009).

Some researchers have discussed the accumulation of a large number of behavioural traits (e.g. knowledge of different foods) as cumulative culture (van der Post & Hogeweg, 2008). However this accumulation does not necessarily involve modifications over time, nor any ratcheting up in complexity or efficiency. Cumulative culture may occur alongside the accumulation of knowledge or behaviour patterns, but there is a key difference between the two. Henceforth, we describe as *accumulation,* the addition of knowledge or behaviour patterns to the behavioural repertoire of an individual or population (akin to 'step-wise traditions', as proposed by Tennie et al. (2009)), and restrict use of the phrase *cumulative culture* to the modification, over multiple transmission episodes, of cultural traits (behavioural patterns transmitted through social learning) resulting in an increase in the complexity or efficiency of those traits.

IV. EVIDENCE FOR CUMULATIVE CULTURE.

(1) Human cumulative culture

(a) Historical evidence

Human culture is clearly cumulative, with innovations being built upon the knowledge of previous generations and ideas from different disciplines and populations combined to formulate new traditions and technologies. Lehman (1947) and Basalla (1988) have both documented the invention, refinement and propagation of novel innovations across various technological and academic disciplines (see also: Ziman, 2000). Lehman (1947) found that there had been rapid advancement in the academic fields of chemistry, genetics, geology, mathematics, medicine and public hygiene, education, entomology, botany, philosophy, operatic and symphonic music. Using historical sources documenting the number of books published or the number of 'outstanding contributions' to a field as judged by several recognised historians, Lehman has demonstrated exponential growth in these fields on an historical timescale (starting between 1000–1600 AD through to the 20th century). Although Lehman's data may be somewhat subjective, he obtained data from multiple sources on the definition of an 'outstanding contribution' in a particular field. He illustrates that by building upon previous knowledge, humans have accelerated their discovery of knowledge. Indeed he predicted that in the near future this acceleration would continue and mechanisation would become more important and widespread, a prediction that, superficially, appears to be true. While Lehman (1947) does not explicitly examine whether cumulative culture is occurring, it is reasonable to assume that the contributions reviewed are built on previous contributions (Enquist et al., 2008).

Basalla (1988) documents how many innovations, often characterised as invented by ‘geniuses’, are part of a continuum of technological development and application of old technology to new areas. For example, Whitney’s cotton gin, which was patented in 1794 and was used to separate short staple cotton from pods, built upon a long line of Indian charkhi machines that had separated long staple cotton from pods, and other agricultural and milling machinery that was available at the time. Similarly, when Guglielmo Marconi received a Nobel Prize in 1909 for transmitting radio signals across the English Channel and the Atlantic Ocean he had built upon, and applied, the pioneering research of physicists such as Hertz and Righi (Basalla, 1988).

Whilst these historical sources illustrate that human culture is cumulative, with notable inventions building on the ideas of others, they do not provide experimental evidence of cumulative modifications to cultural traits.

(b) Human empirical work

Several researchers have investigated cumulative modifications to behavioural traits using artificial 'generations' in the laboratory. In these diffusion chain experiments, participants take part in a task in series; thus the first participant will act as demonstrator to the second participant, who will in turn act as demonstrator to the third participant and so forth (see Mesoudi & Whiten, 2008 for a review).

Kirby et al. (2008) set up a diffusion chain experiment in which novel words (sequences of lower-case letters) were paired with coloured shapes with an arrow indicating a movement pattern. Individuals were trained with a set of shape/movement and word pairs. They were then tested, having to write down the words paired with both previously seen shapes/movements and, unknown to the participant, unseen shapes/movements. As mistakes in recall of shape/movement and word pairs were made across 'generations' in the experiment, the artificial language became less diverse with an accompanying reduction in transmission errors. Indeed, in some chains transmission errors were reduced to zero as languages increased not in complexity but in ‘learnability’. Over the course of the experiment, the structure of the ‘language’ increased, with words for each colour and each movement type increasing in similarity. This increase in structure, the authors suggest, was the reason why the language was transmitted with fewer copying errors. They also argue that the increased structure, representing an increasingly efficient artificial language by the end of the experiment, represents cumulative improvement in the trait.

Also using a transmission chain design, Flynn (2008) presented children with puzzle boxes in which a reward was held in place by a series of defences. Children received an initial demonstration containing both task irrelevant actions (which had no bearing on gaining the reward) and task relevant actions (which allowed reward retrieval). The aim was to assess whether children would copy both the functional and non-functional actions, or whether the irrelevant actions would be filtered out gradually along the diffusion chain. Flynn found that children did parse out task irrelevant actions, often quite early in the diffusion chains. Thus the technique that the children employed was gradually modified across the laboratory ‘generations’, creating a more efficient means to gain the reward. Flynn (2008) argues that this modification of the procedure represents a cumulative improvement in efficiency and, therefore, a cumulative cultural process.

Much of the laboratory-based evidence concerning cumulative increases in the complexity of human (simple) technologies has been provided by Caldwell and colleagues (Caldwell & Millen, 2008; Caldwell & Millen, 2010b). Experimental micro-populations were set simple tasks, such as making paper airplanes or constructing towers with uncooked spaghetti and plasticine. Participants were told the aim was to build a plane that flew as far as possible or a tower that was as tall as possible. By using overlapping laboratory generations in the population, of variously two to four individuals, they were able to expose naïve individuals to skilled individuals. Using this ‘micro-society’ replacement design, they found that over 'generations' the performance of the technology (the mean distance flown by a plane or the mean height of a tower) increased. Designs within chains were more similar than those between chains, suggesting the formation of traditions, with individuals learning socially about design aspects of the technology.

A striking finding was that the level of conservatism of design was higher when pay-offs were less predictable (Caldwell & Millen, 2010a). In this experiment there were two measuring protocols; in one condition spaghetti towers were measured immediately upon completion, whilst in a second condition the towers were measured five minutes after completion and following their transfer to a table upon which was a desk fan. The increase in uncertainty about whether the tower would remain standing in the breeze from the fan decreased the amount of modification made to designs over the chain compared to towers that were measured immediately, raising the possibility that in more risky situations the ratcheting up of cumulative cultural traits may be hindered.

Caldwell and Millen (2009) applied the transmission chain design to examine the mechanisms underlying cumulative changes in cultural traits, in this case making paper airplanes. Participants were assigned to one of several conditions in which they could gain information through different mechanisms, by observing others construct planes (imitation), teaching, and seeing the planes others had made (emulation), or a combination of these mechanisms. They found that any one of these mechanisms was sufficient to elicit a cumulative improvement over the laboratory generations. It remains to be seen whether this pattern is characteristic of multiple tasks, particularly more complex tasks. Plausibly, high-fidelity information transmission (e.g. as is potentially facilitated by language, teaching or imitation) might be necessary for the transmission of more complicated technology.

The empirical study of cumulative cultural changes in humans is relatively young, but the results so far give an interesting insight into the process. A moot point is whether these findings will hold up when more challenging tasks, those less likely to be invented by a single individual, are deployed.

(2) Non-human cumulative culture.

Compared to the empirical investigation of cumulative culture in humans, that in other animals is both scarce and controversial.

(a) Evidence from the wild

Based on observations of animals in the wild, some researchers have claimed that other species show cumulative culture. As these observations must allow a comparison with the cumulative culture that is observed in humans, we suggest the following criteria be deployed to guide identification of cumulative culture in other animals. First, there should be evidence that the behavioural pattern or trait is socially learned and any variation in the character is not solely due to genetic or environmental factors (Laland & Janik, 2006). Second, there must be evidence that the character in question changes over time in a directional, or progressive manner. This requires evidence that it has been transmitted between individuals through social learning over repeated episodes. It also requires evidence that the character has changed in the transmission process to achieve an enhanced level of complexity. For practical reasons, a useful yardstick is that the character should be beyond what a single individual could have invented alone (Tennie et al., 2009) (Table 1). The evidence for cumulative transmission may come from long-term field studies, archaeological finds or some other source. However, we emphasize that the occurrence of similar, but non-identical, behaviour patterns in different populations (whether for the same purpose or different purposes), does not constitute evidence that one evolved from the other, and that supplementary evidence (e.g. observational, archaeological) will be required to demonstrate that variation in the character is attributable to ratcheting, and that cumulative change occurs within a historical lineage. The appearance of similar methods for performing a task in different populations may reflect the fact that there is a salient, or easily-discoverable, method of performing that task and not evidence of shared ancestry. Cultural evolution is likely to occur over a shorter time scale than genetic evolution, which may also alter behaviour, but over a longer time period.

Boesch (2003) proposes three chimpanzee behavioural patterns that he believes show the hallmarks of cumulative modifications. The first is nut-cracking behaviour, displayed by different populations across Africa. In particular, Western populations use tools, such as hammer stones, to crack nuts, and Boesch believes this is an elaboration of an ancestral behaviour pattern of hitting nuts on the substrate to smash them. This behaviour pattern has, according to Boesch, been further modified with the use of anvil stones and, in some cases, a second, stabilising stone. However, the latter claim remains uncorroborated. Moreover, it is unclear whether even the most complex variant of nut cracking, that including hammer, anvil and stabilising stone, is too complex for one individual to have invented (Tennie et al., 2009). Archaeological analyses by Mercader et al (2007) found chimpanzee nut cracking stone technology could date as far back as 4,300 years ago, suggesting that there has been little behavioural modification during that time. Thus, evidence from the archaeological data and contemporary assessment of the behaviour patterns suggest that, even if modifications have been added to nut cracking, these are not obviously more complex than one individual could have invented alone.

The second behaviour pattern outlined as cumulative by Boesch (2003) is ectoparasite manipulation in the three Eastern chimpanzee communities of Budongo, Mahale and Gombe. At all three sites leaves are used to inspect the parasites that have been removed during grooming; at Budongo the parasite is placed on a leaf when removed. However, at Mahale individuals fold the leaf and then cut it with their nail. At Gombe there is a variant in which several leaves are piled on top of one another before the parasite is placed on the top and inspected. However, these are small modifications and there is no direct evidence that what has been described as the 'modified' behaviour pattern is derived from the ascribed 'ancestral' behaviour pattern. Whilst the two hypothetically 'derived' behaviour patterns could each have evolved from the hypothesised 'ancestral' character, it remains possible that each variant could have been invented independently.

The third behaviour pattern highlighted by Boesch (2003) is a modification of the context for an existing behaviour pattern and the possible addition of a separate technology to it. This is the digging of wells in dry environments, which, it is argued is translated to contexts in which water sources are contaminated where the additional use of leaf sponges is observed. The addition of leaf sponging to well digging may be regarded as an increase of complexity of one behaviour pattern, and thus representative of cumulative culture, although it is not clear that the combination of these existing behaviour patterns is outside of the capacity of a single individual to invent. Also, the digging of wells in polluted areas is the application of a known behaviour in a new context (an 'innovation', see Reader & Laland 2003), not an increase in complexity, and represents *accumulation* (as discussed in section III (Tennie et al., 2009)).

Another chimpanzee behavioural trait hypothesised to be the result of modifications to an ancestral trait is the tool set observed in some populations.

The complex tool sets observed at some sites, most notably in the central African communities, appear to be used, in sequence, for different aspects of the same foraging behaviour (Sanz & Morgan, 2007; Boesch et al., 2009; Sanz & Morgan, 2009; Sanz et al., 2009). One tool is normally used to puncture the outside of a nest of ants or bees. Other tools are then used to widen the hole to allow greater access to the food within. Finally, a smaller stick tool is used to gather honey, ants or larvae. In one study this 'collector' stick was modified to increase the surface area (Boesch et al., 2009; Sanz et al., 2009), the bark being removed and the wood below chewed to make it more brush-like. These tool sets contrast with other populations in which similar behaviour is performed, but with a single tool (Whiten et al., 1999; Humle & Matsuzawa, 2002). Once again, there is no direct evidence that any of the single tool or proposed 'simpler' behaviour patterns are ancestral to the multiple tool or more elaborate variants. Whilst these tool kits may be a case of simple cumulative culture, without the required evidence it is currently not clear that they are more complex than a single individual could invent alone.

Perry et al. (2003) reported a number of social conventions that arose in a population of capuchin monkeys that are also suggestive of cumulative culture. These social games appear to have derived from the existing hand-sniffing behaviour (Perry et al., 2003), which has been observed in some populations. The social games, the hand-in-mouth, hair-in-mouth and toy-in-mouth games emerged in succession, within one group, with the latter two appearing to be modifications of the first (Perry et al., 2003). However, whilst this represents an interesting case of modifications to a social behaviour pattern, all modifications appear to have been initiated by one individual, Guapo, a young male in the group. Although this demonstrates the ability of individuals in the species to make small modifications to a behaviour pattern, it does not represent a multi-generational or even multi-individual behavioural modification. Thus, in the absence of evidence for repeated bouts of transmission and refinement, this example too fails to provide clear evidence for cumulative culture, and is better characterized as several bouts of individual learning building upon one another.

More recently, white faced capuchins have been observed performing the 'eye poke' social convention, documented as the poking of a conspecifics finger into the eye of another (Perry, 2011). 'Eye poking' (to oneself) has interestingly been reported to occasionally occur concurrent with the 'hand sniff' (Perry, 2008), representing conjunction of the two conventions. Importantly however, this eye poke convention, along with the other reported social conventions, seem to have been reinvented in different groups/locations (Perry, 2011), providing further support that these behaviours are not beyond what individuals can invent for themselves. Moreover, there is as of yet no evidence that eye-poking with hand sniff is in any sense superior to the hand sniff alone, which means this variation may well be better characterised as cultural drift (in which random changes have occurred, without selection). Hence, these examples, while representing interesting social traditions, cannot yet be said to be cumulative. Stone-handling behaviour in Japanese macaques is present in different forms at sites throughout Japan, although its adaptive significance is unknown (Leca et al., 2007; Huffman et al., 2008; Nahallage & Huffman, 2008; Leca et al., 2010). Some variants of the behaviour are almost ubiquitous, while others are rare, leading to the hypothesis that some individuals may be specialists, who have created new behavioural variants from existing ones (Leca et al., 2007). However, once again, there is no evidence that even the most complex of the stone-handling behaviours is outside a single individual's capacity to invent, and the putative refinements are not unambiguously improvements. If these traits are non-adaptive, as it is claimed (Leca et al., 2007), then there would seem to be little reason for there to be conservatism in the behaviour and, therefore, we might expect to see great diversity in stone-handling modifications in Japanese macaques through a drift-like process (Caldwell & Millen, 2010a). This would mean that, rather than any one stone-handling behaviour building in complexity (or efficiency) upon another, each behaviour may simply represent the corruption of an existing stone-handling behaviour, inaccurately transmitted between individuals, without any further addition of complexity. Note that, we do not dismiss accidental mutations or inaccurate transmission as playing a role in cumulative culture but, that for ratcheting to occur beneficial 'accidents' would be preferentially retained.

Circumstantial evidence for cumulative modifications can also be found in New Caledonian crows (Hunt & Gray, 2004; Seed et al., 2007). The species uses several tools, the most studied of which are constructed from *Pandanus* leaves, which are used for foraging. Hunt and Gray (2003) document three different designs of these tools: narrow, wide and stepped. Amongst the stepped designs, between one and four steps are used. These patterns vary geographically across New Caledonia. It has been claimed that the variation in *Pandanus* tool design across New Caledonia is most parsimoniously explained as cumulative variation (Hunt & Gray, 2003). Hunt and Gray (2003) propose that the wide tools are the ancestral tools with the narrow and stepped types derived from them. The variation in stepped tools has also been proposed to be a series of modifications to the original one step design (Hunt & Gray, 2003). However, like chimpanzee's tools, there is no direct evidence that these lineages are correct and the different tool types are not individual innovations, each invented from scratch. The evidence for social learning in the wild is also equivocal, suggesting there is a significant level of individual invention (Holzhaider et al., 2010) and evidence from captivity indicates New Caledonian crows may possess an inherited predisposition for tool use and tool manipulation (Kenward et al., 2005; Kenward et al., 2006).

The difficulties of interpreting putative examples of cumulative culture in wild populations, as summarised in Table 1, being at the same time suggestive but inconclusive, has led some researchers to work on captive populations, to examine experimentally whether animals are capable of cumulative cultural learning.

Insert Table 1 about here

(b) Empirical testing of non-human cumulative culture.

The first explicit test of the capacity for cumulative cultural learning in non-human primates found little evidence that chimpanzees could accumulate modifications to their behaviour (Marshall-Pescini & Whiten, 2008). This test involved a puzzle box that could be opened in two ways, with the second, more complicated, method allowing access to nuts and a greater volume of honey than the first, simpler method, which just allowed animals to dip for honey. The chimpanzee subjects were allowed to manipulate the puzzle box in a baseline condition with no demonstration, resulting in two individuals out of 14 discovering the first, ‘dipping’ method, and one also discovering the more complicated method. When the dipping method was demonstrated by a familiar human demonstrator three more individuals managed to learn it. These animals then received a demonstration of the more complicated method; of the five individuals tested only one performed the more complicated method and this was the individual who had already discovered the method in the baseline trials.

Researchers have also drawn conclusions about cumulative culture from the results of experiments investigating other cognitive factors in chimpanzees. In an experiment in which subjects were required to obtain food by pushing it around a maze using a stick, five individuals discovered that by rattling the board on which the maze was placed, food could be obtained more rapidly (Hrubesch et al., 2009). The researchers altered the conditions in which animals could interact with the maze board, either taking away sticks to encourage the rattling technique, or bolting the maze down to prevent the rattling technique. They found that individuals did not switch the technique they used and appeared to have become fixed upon the method they had already discovered. The authors argue that this behavioural conservatism may explain the lack of cumulative cultural evolution in non-humans.

Compound tool use, the combining of separate objects to make a meta-tool, has been observed in wild chimpanzees, on a handful of occasions and only in certain contexts (Sugiyama, 1997; Boesch, 2003). Price et al. (2009) tested captive chimpanzees, where subjects were required to put together two component tools to create an elongated single tool that could be used to retrieve an out-of-reach food reward. Chimpanzees were significantly more likely to learn to combine and use the tool when they had seen a video demonstration showing the tool being manufactured and used, than in other conditions, where individuals received a video demonstration of only part of the process. This suggests that the participants were able to modify a tool, which they then used to retrieve food and may have the potential for rudimentary cumulative cultural learning. However, as some control subjects, who received no demonstration of the combining process, were also able to learn to make the complex tool, it clearly is not beyond a single individual's capabilities (Tennie et al., 2009).

The most comprehensive experimental attempt to investigate the factors that may underlie cumulative culture in animals to-date was carried out by Dean et al (2012). In a comparative study of sequential problem solving, Dean et al provided groups of capuchin monkeys, chimpanzees, and nursery school children with an experimental puzzle box that could be solved in three stages to retrieve rewards of increasing desirability (Figure 1). Stage 1 required individuals to push a door in the horizontal plane to reveal a chute through which a low-grade reward was delivered. Stage 2 required individuals to depress a button and slide the door further to reveal a second chute for a medium grade reward. Stage 3 required the solver to rotate a dial, releasing the door to slide still further to reveal a third chute containing a high-grade reward. All stages could be completed through two parallel options, with sets of three chutes on both left and right sides. This two-action, two-option design aided evaluation of alternative social learning mechanisms and allowed two individuals to operate the puzzle box simultaneously. After 30 hours of presentation of the task to each of four chimpanzee groups, only 1 of 33 individuals reached stage 3, with a further 4 having reached stage 2, and with each group having witnessed multiple solvers at stage 1 (experiment 1). Chimpanzee performance was not greatly enhanced by trained demonstrators (experiment 2). A similar pattern was observed in the capuchins: after 53 hours, no individual reached stage 3 and only two individuals reached stage 2. Thus, the experiments provided no evidence for cumulative learning in chimpanzees or capuchins. These findings stand in stark contrast to those of the children, where despite a far shorter exposure to the apparatus (2.5 hours), five out of eight groups had at least two individuals (out of a maximum of five) who reached stage 3, with multiple solvers at stages 2 or 3 in all but two groups. Dean et al found that the success of the children, but not of the chimpanzees or capuchins, in reaching higher-level solutions was strongly associated with a package of sociocognitive processes—including teaching through verbal instruction, imitation, and prosociality—that were observed only in the children. Children's individual task performance covaried strongly with the amount of teaching, imitation and other prosocial behaviours (donation of retrieved stickers) they personally received; those children that received less support were less likely to get to the higher cumulative stages of the task and all children who got to the final stage did so with, usually, at least two forms of social support (Dean et al., 2012). Thus, completion of all stages of the task was beyond that which an individual child could invent for his/herself. While this study does not represent a multi-generational approach, it provides evidence for the socio-cognitive factors necessary for cumulative learning to occur, and provides evidence of repeated bouts of elaboration and social transmission amongst the children.

Insert Figure 1 about here

In summary, at present, reports of cumulative culture in animal species remain subjective and circumstantial. Observations from the wild and captivity suggest that while some species are capable of modifying behaviour, these modifications do not seem to accrue across generations and do not clearly move beyond what individuals alone can invent for themselves (see also: Tennie et al., 2009). This suggests that while animals can transmit behaviour socially to create localized traditions, animal cultures are either not cumulative at all or cumulative in a highly restricted and simple respect.

V. WHY ARE THERE DIFFERENCES IN CUMULATIVE CULTURE BETWEEN HUMANS AND NON-HUMANS?

The evidence that cumulative cultural evolution may be unique to humanity has led researchers to construct various hypotheses as to the critical processes that underpin human cumulative culture.

(1) Hypotheses concerning the lack of cumulative culture in non-humans.

Some of the hypotheses focus upon species differences in social structure and inter-individual tolerance that might plausibly affect the spread of cumulative innovations. Others focus on cognitive mechanisms that may affect the constituent processes of cumulative culture.

(a) Cognitive differences

The distribution of cumulative culture may be accounted for by the presence of cognitive mechanisms specific to, or substantially enhanced in, humans.

However, researchers do not agree which particular processes are unique to humans and which may promote cumulative culture.

(i) Innovation: An increased creativity, that is the ability to innovate, has been proposed to drive cumulative culture. Enquist et al. (2008) argue that cultural traits must be invented to spread within the population and be modified in a cumulative process. Whilst this argument is logical, there are extensive data documenting innovations in a range of species of primates (Reader & Laland, 2002) and birds (Overington et al., 2009), yet comparatively little evidence for traditions and cumulative culture. This data suggests that innovation alone is not sufficient for cumulative culture. Indeed, a recent study suggests that innovation may act as a cultural catalyst, at least in the early stages of ratcheted technologies, functioning only to speed up the level of cultural complexity attained (Pradhan et al., 2012).

(ii) Conservatism: In contrast to the creativity of humans, it has been argued that non-humans are conservative in their actions. Some experimental studies have reported that non-humans, in particular chimpanzees, continue to use the first solution they discover even when a potentially more rewarding alternative is available to them (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009; Whiten et al., 2009). A recent demonstration of conservative behaviour in chimpanzees was provided by Hopper, et al. (2011). In this study, chimpanzees preferentially exchanged the token they had seen a conspecific model exchange for food, even when the food received was of lower value than that which a second, alternative, token yielded. Interestingly, the two potential outcomes

(high or medium value rewards associated with the two token types) were gained using the same behaviour (token exchange), yet there was little evidence of chimpanzees switching between the tokens despite all gaining experience with the alternative token, which in one group yielded the high value rewards. However, the extent to which the two behavioural options were understood by the chimpanzees is unclear. Likewise, the role of the identity of the model in enhancing this conservatism is yet to be investigated, and may prove explanatory given that both models were of relatively high rank (Kendal et al. in prep)

Researchers have argued that the discovery or utilisation of a more rewarding solution is suppressed by the initial discovery of a task solution (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009; Whiten et al., 2009; Hopper et al., 2011). Similar arguments concern a species propensity for functional fixedness, that is the inability to use items beyond their initially learnt affordances (Hanus et al., 2011). Specifically, it is thought that functional fixedness can occur from one's own experience with environmental features, canalising its use according to how such was personally used in the past. Alternatively, normative influence may play a role, such that one's cultural background or norms for item affordances could inhibit learning new item functions (Gruber et al., 2011; Hanus et al., 2011). According to these arguments, cumulative additions to a solution would be increasingly likely to occur in species as conservatism (and/or functional fixedness) decreased. Wood et al. (2013) have recently shown that children acquire multiple strategies to a problem, even where their first solution procured a reward of no lesser value than the alternative solutions they went on to use. Therefore, if humans are less conservative than chimpanzees, as suggested by Whiten et al. (2009), this may partly explain the prevalence of cumulative culture in the former relative to the latter. However, the aforementioned study of cumulative problem solving, in children, chimpanzees and capuchin monkeys (Dean et al., 2012), found no evidence for conservatism or behavioural inflexibility in any of the species.

It is important, here, to distinguish between conservatism as a mechanism and as an outcome. For example, if a species lacks the capability to copy in proportion to behavioural payoffs, beneficial demonstrated solutions may be neglected in favour of previously learned and rewarded solutions. Thus animals would fail to elaborate upon acquired behaviour and would consequently appear 'conservative'. Conservatism, as a mechanism, however, posits that there exists a specific conservative learning strategy on the part of the animal.

Interestingly, behavioural flexibility rather than conservatism has recently been documented in captive orangutans. Lehner et al. (2011) investigated orangutans' (*Pongo pygmaeus abelii*) ability to modify previously used techniques when the previous behaviours were blocked. Three conditions were presented in which orangutans could retrieve syrup from a tube employing various tool methods, the two later conditions were successively more restrictive, forcing animals to alter the method they had used previously. The animals did switch to new techniques for gaining the food reward, demonstrating behavioural flexibility. The authors claim that two of the techniques built cumulatively upon other techniques, however there is no evidence that these new techniques were socially transmitted.

(iii) Imitation: The fidelity of transmission of behavioural traits between individuals has been proposed to be of key importance to the evolution of

cumulative culture (Boyd & Richerson, 1985; Galef, 1992; Tomasello, 1994; Lewis & Laland, In Press). Imitation, learning the exact motor pattern of a behaviour from observing another individual, is argued by some researchers as central to human cumulative culture (Tomasello, 1994; Boyd & Richerson, 1996; Tomasello, 1999), since it is the social learning process capable of supporting high-fidelity transmission. Thus individuals do not have to 'reinvent the wheel' when they learn a new behaviour.

Recent theoretical work suggests that imitation is not necessary for non-cumulative traditions, which can emerge from simple learning processes, such as local/stimulus enhancement coupled with reinforcement learning or from asocial learning when individuals are exposed to the same environment (van der Post & Hogeweg, 2008). These learning mechanisms, while sufficient to support durable traditions (Matthews et al., 2010) or an *accumulation* of behavioural traits (van der Post & Hogeweg, 2008), would seem an insufficient foundation for cumulative culture insofar as enabling the accumulation of beneficial modifications to an existing behavioural trait, increasing its complexity. To the extent that local/stimulus enhancement results in low fidelity transmission, as is widely thought (although we note there is little hard data here), then Lewis and Laland's (In Press) theoretical analysis would not expect it to result in cumulative culture. Thus, if a species is not capable of accurate imitation (or teaching) it is much less likely that it will be able to develop cumulative culture. In support of this theory, Dean et al. (2012) found that between species (capuchins, chimpanzees and children), and within species, performance with a cumulative problem-solving task correlated strongly with the degree of task manipulations performed by individuals that matched those of their predecessors at the task. It is noteworthy, however, that end state emulation can result in high-fidelity social learning and thus imitation may not be as essential for cumulative culture but rather high fidelity learning in general (Caldwell et al., 2012). However, end state emulation may result in high fidelity learning only in those tasks for which the end product can readily be recreated from viewing the action's products, while imitation is required for process-opaque tasks (Acerbi et al., 2011; Derex et al., 2012). Object movement emulation may constitute another route to high fidelity learning. For example, it has been shown that after viewing video footage of physical object movements only, through digital removal of a demonstrator's behaviour, children's object movements were comparable to when a full behavioural-object movement demonstration was viewed (Huang & Charman, 2005). Task difficulty and task demands are however likely to play an important role in whether forms of emulation are sufficient to optimise behaviour (Acerbi et al., 2011).

Why, then, when there is recent evidence that chimpanzees are capable of imitation (Whiten et al., 1996; Horner et al., 2006; although see Tennie et al., 2012), do they not appear to have developed cumulative culture? There are various potential explanations for this. First, while chimpanzees have shown some capacity for imitation this may be the exception rather than the rule, with other social learning mechanisms such as emulation or stimulus enhancement, associated with lower copying fidelity, responsible for much behavioural propagation (Tomasello, 1999; Tennie et al., 2009; Hopper, 2010; although see Caldwell et al., 2012). Moreover, comparative studies reveal substantive differences in the amount of imitation, and rate of imitative learning, exhibited by humans and chimpanzees (Horner & Whiten, 2005; Herrmann et al., 2007;

Dean et al., 2012; Hecht et al., 2012), suggesting that while chimpanzees may be capable of imitation, they are not as proficient at it (or perhaps, as motivated to imitate) as humans. Second, there is a lack of evidence that when imitating chimpanzees formulate the copied agent's intentions (Tomasello & Carpenter, 2007). That is, compared to humans, chimpanzees may be less capable of rational imitation, or may be less able to imitate actions deliberately and consciously in order to achieve the same outcome as that inferred for the demonstrator. The ability to take into consideration the demonstrator's goals and intentions might plausibly facilitate cumulative culture, if this increased the accuracy of information transmission (although see arguments regarding imitation of irrelevant actions, or 'overimitation' in children (Horner & Whiten, 2005; Lyons et al., 2007; Lyons et al., 2011).

(iv) Adaptive filtering: Enquist and Ghirlanda (2007) argue that imitation alone cannot support cumulative culture. They argue that in the absence of adaptive filtering mechanisms, or strategies evaluating the consequences of observed behaviour, blind or random imitation is likely to occur. This creates a situation in which maladaptive traits are as likely to spread as adaptive traits. However, if individuals use rational imitation (Carpenter et al., 1998; Gergely et al., 2002) or reliable learning heuristics (Laland, 2004) dictating what (and whom, e.g. (Wood et al., 2012) is copied, the replication of maladaptive or suboptimal traits could be reduced. In the case of chimpanzees, the absence of cumulative cultural evolution, may also be related to an inability to evaluate the consequences, or payoffs, of observed behaviour. It has yet to be established whether chimpanzees, and indeed other animals, possess an adaptive-filtering process

that serves to remove maladaptive behaviour, but there are reasons for doubting that this is the key to the absence of cumulative culture in animals. That is because the demonstrating animals themselves are likely to exhibit adaptive filtering, since individuals disproportionately perform productive, high-payoff behaviour, leaving the pool of variants available to copy a selective set of tried-and-tested solutions (Rendell et al., 2010).

(v) Teaching: Teaching is behaviour that functions to impart knowledge, and differs from other forms of social learning in requiring an active and costly investment by the tutor into the learning of the pupil (Caro & Hauser, 1992). Teaching frequently requires the teacher to infer the current knowledge state of the pupil to allow an appropriate level of support (Flynn, 2010); however, inferring knowledge states in other animals is difficult. The distribution of teaching may be wider than previously thought, with experimental evidence in meerkats, pied babblers, ants and bees (Franks & Richardson, 2006; Thornton & McAuliffe, 2006; Raihani & Ridley, 2008), although whether the teaching in non-humans is consanguineous to human teaching remains debatable (Premack, 2007; Hoppitt et al., 2008). Teaching may be particularly important for the transfer of cumulative modifications, as it functions to promote the fidelity of knowledge transfer, potentially allowing specific behavioural patterns to be transmitted between individuals until such a time as beneficial modifications appear (Boyd & Richerson, 1985; Tomasello, 1999). Indeed, teaching can be characterized as behaviour that functions specifically to enhance the fidelity of information transmission. A recent mathematical analysis of the evolution of teaching (Fogarty et al., 2011) found that cumulative culture broadens the range

of conditions under which teaching is favoured by selection, leading to the hypothesis that teaching and cumulative culture may have coevolved. This finding is consistent with the findings of the aforementioned experimental investigation of cumulative culture (Dean et al., 2012), which reported strong positive correlations between how much teaching a child received from other children and how well they performed on the cumulative culture puzzle box task.

(vi) Complex communication: Alongside teaching, human language, a uniquely complex communication system (Tomasello, 1999; Hauser et al., 2002; Pinker & Jackendoff, 2005; Cheney & Seyfarth, 2010), may promote cumulative culture, again through facilitating accurate transmission. Language allows the transmission of intentions and complex behaviour patterns between individuals and the facilitation of easy and 'cheap' pedagogy; greatly enhancing teaching. Language has also enabled humans to compile written records of the beliefs, ideas, innovations and technologies of our predecessors, which provides protection against cultural loss, as well as enabling access to the knowledge of individuals that are outside individuals' social networks. Language, both in the form of verbal and linguistic notation therefore, could enable high-fidelity transmission of modifications to existing behavioural traits, facilitating cumulative culture (Tomasello, 1999; Csibra & Gergely, 2005; Tomasello et al., 2005; Carpenter, 2006). Consistent with this, Dean et al. (2012) found that children's performance in the cumulative task covaried with the amount of verbal instruction they received from other children.

(vii) Prosociality: The evolution of prosociality, enabling cooperation between individuals, increased tolerance, and the shared motivations of individuals has been proposed to support the evolution of cumulative culture (Tomasello & Call, 1997; Tomasello, 1999; Tomasello et al., 2005; Tomasello & Moll, 2010). The argument states that if individuals cooperate they will be able to work on a task together, allowing naïve individuals to get closer to and thus learn from a knowledgeable individual (Tomasello & Call, 1997). Working together also allows two or more individuals to discover solutions to a task and to pool their information, thus providing the opportunity for two separate solutions to be combined or modified (Tomasello, 1999). If individuals share motivations they are able to recognise that another individual has a goal and intentions, and potentially are able to assist others to achieve their goal (Tomasello et al., 2005). Shared intentionality, in which individuals recognise that others, who may not even be present at the time, share their goals and intentions, can facilitate the modification of a behaviour pattern by many individuals, over many transmission episodes and, therefore, the evolution of cumulative culture (Tomasello et al., 2005; Tomasello & Moll, 2010). Indeed, Dean et al. (2012) also highlighted a significant role for prosocial behaviour (donation of retrieved rewards to others) in the success of children in their cumulative problem-solving task. These authors hypothesized that such prosocial behaviour signified an understanding of shared motivations and served to scaffold the learning of naïve individuals.

In summary, a number of cognitive differences have been proposed to explain the evolution of cumulative culture. However, it seems unlikely that one cognitive trait could explain the evolution of cumulative culture by itself. Instead there may be differences in a suite of cognitive traits between species (e.g. socio-cognition: teaching, imitation, pro-social behaviour and complex communication, (Tomasello, 1999; Dean et al., 2012)), which collectively afford the high-fidelity information transmission, social tendencies, and motivations necessary for cumulative culture.

(b) Social learning strategies

Whilst social learning may often provide a cheaper and quicker method of learning than asocial learning (Rendell et al., 2010), theoretical models suggest that it should not be used indiscriminately (Boyd & Richerson, 1985; Laland, 2004). Rather, to enhance fitness individuals should use social learning strategies, or cultural transmission biases, to dictate when to collect social information and from whom to acquire it (Boyd & Richerson, 1985; Laland, 2004; Kendal et al., 2005; 2009b). Certain social learning strategies have been proposed to be important to the evolution of cumulative culture.

(i) Conformity: One such strategy is conformity, defined as the propensity to disproportionately copy the most frequent behavioural trait in the population, over and above the chance expectation (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Whiten et al., 2005). Our definition of conformity differs from that deployed in social psychology, which focuses on the normative and social influence acting on the copying of (incorrect) decisions, originating from the work of Asch (1955), (Morgan & Laland, 2012). Mathematical models reveal that conformity is favoured under a very wide range of conditions (Henrich & Boyd, 1998) and contributes to the high-fidelity transmission required for cumulative

culture. However, Eriksson et al. (2007) found that conformity hindered the spread of adaptive variants, with individuals who adopt cultural traits at random being more successful than those who adopt a conformist strategy. Eriksson et al.'s model encompasses temporal variation in the environment but not a spatial component, thus preventing sub-populations from forming and, therefore, conformity from evolving within them. Thus the model fails to provide a realistic approximation of human demography and the geographical parameters that influence behaviour and trait transmission.

Conformity, defined as copying the behaviour displayed by the majority of individuals rather than disproportionate copying of the behaviour of the majority, was recently shown in chimpanzees and 2-year-old children (Haun et al., 2012). Specifically, after observing three conspecifics demonstrate the same behaviour (each dropping a ball into a coloured box) or one individual demonstrate a different behaviour three times (drop a ball three times into a different coloured box), chimpanzees and children copied the behaviour of the majority. In contrast, orangutans showed no such majority biased copying when exposed to the same experimental procedure. While this study makes an initial step towards investigating general majority biased transmission in different primate species', the interpretation of this data is open to debate (pers. comm. Tom Morgan). As noted by Haun and colleagues (2012), further investigation in this area is needed, particularly to isolate the influence of unbiased or random copying in such tasks, as unbiased copying itself is frequency dependent. The testing of conformity bias, defined as a disproportionate likelihood of copying the most frequent trait in a population, is required before drawing conclusions on the effect conformity has on other animals' social transmission and their opportunities for cumulative culture. Furthermore, avoidance of the minority response or the undemonstrated option could have played a role in the behavioural responses observed in chimpanzees and children (pers. comm. Tom Morgan). Further data will help clarify majority biased learning in these species.

Kandler and Laland (2009) modelled the spread of cultural traits, derived through independent innovation or cumulative modification, with different levels of conformity bias (defined as disproportionately copying the most common cultural variant) to the transmission of the traits. They found that strong conformity (in which it was difficult for frequency-independent traits to invade) tended to hinder the spread of novel innovations within the population, irrespective of whether the innovation was beneficial or not, as individuals would fail to switch to a new variant. Conversely, under a weaker conformity bias a beneficial variant could spread within the population. Some individuals would switch after determining that the new variant was more beneficial, and this was enhanced as the trait became more common by individuals using a conformist learning bias. Weak conformity was, therefore, suggested to be adaptive, since it resulted in a greater proportion of individuals adopting the beneficial variant. Such ‘weak conformity’ is apparently supported by the equivocal or conditional empirical evidence for conformity in humans (Coultas, 2004; McElreath et al., 2005; Efferson et al., 2007; Efferson et al., 2008; McElreath et al., 2008; Eriksson & Coultas, 2009; Morgan et al., 2012). Thus the impact of conformity, and, indeed, the extent to which species do conform, is currently unclear.

(ii) Selective copying: Mathematical models have also suggested that selective

copying of successful behaviours or successful individuals, when coupled with the opportunity to learn asocially, can strongly affect cumulative cultural evolution (Ehn & Laland, 2012). Ehn and Laland propose an 'individual refiner' strategy, which first uses social learning, and then refines through individual learning, and continues to do so irrespective of the level achieved. This strategy generates high fitness across a broad range of conditions, leads to high amounts of socially transmitted behaviour in the population, and accumulates significantly more innovations over the generations than other strategies.

Wisdom and Goldstone (2010) recently demonstrated this sensitivity to the performance of others in the laboratory by exposing human participants to a computerized game. When trying to solve the game, participants had access to the choices of the other participants and could choose to copy their task solutions. The investigators also manipulated whether participants could see the payoffs relating to the task solutions of the other participants. Overall the results indicated that when neighbour scores were visible, groups attained higher overall scores with more pronounced cumulative improvement across rounds than those in the invisible score condition. These results indicate that identifying and copying successful individuals may play an important role in human cumulative evolution.

Likewise, Morgan et al. (2012) exposed humans to a series of cognitive puzzles, in which they were able to view the choices of others. In addition to conformist transmission, they found that participants were able to improve their performance using a proportional observation strategy, copying demonstrators in proportion to the level of reward the demonstrator received (Schlag, 1998).

The participants also used (conditional) proportional imitation strategies, whereby individuals copy the behaviour of others in proportion to how much better the other's payoff is than their own (Schlag, 1998). Game theory analysis has established that this strategy optimises cumulative cultural learning (Schlag, 1998).

Empirical evidence of the presence of 'copy successful behaviour' and 'copy if dissatisfied' strategies in nonhuman animals is currently limited to a handful of studies. Galef et al. (2008) reported evidence for a 'proportional reviewing' strategy, as set out by Schlag, (1998), in female Norway rats (*Rattus norvegicus*). Rats who were exposed to energetically dilute diets, displayed a greater propensity to copy the food choices of demonstrator rats than energetically satisfied rats, with the propensity to copy being proportional to the level of nutritional deprivation. However here the dissatisfaction was not with regard to the payoffs of a particular behavioural trait and the copying behaviour may also be interpreted as a manifestation of a 'copy when uncertain' strategy in nutritionally deprived rats (Kendal et al., 2009c).

There is also some evidence that nine-spined sticklebacks (*Pungitius pungitius*), adopt a proportional observation strategy (Kendal et al., 2009a; Pike et al., 2010). After gaining personal experience of two food patches, containing different densities of food, focal fish observed conspecifics feeding at the same resource sites, however the food densities of the patches were manipulated, such that the fish's personal experience no longer predicted the food density. When subsequently given the choice of food patch, focal fish tended to copy the social information in proportion to the demonstrators' payoff (Kendal et al., 2009a; Pike et al., 2010).

Social learning strategies depend upon the underlying cognitive capacity for social learning and may also be influenced by social structure and tolerance. Given the evidence for social learning strategies in other animals, it seems unlikely that social learning strategies alone could explain the evolution of cumulative culture. However, it is possible that humans may implement particular strategies, such as payoff-based copying, more efficiently, by virtue of their possessing higher-fidelity transmission mechanisms.

(c) Social structure

In humans, differences in population size, connectedness and social structure are thought to alter the ease with which complex behaviour patterns can be transmitted between individuals, thus accounting for the observed distribution of cumulative culture (Powell et al., 2009; Kline & Boyd, 2010; Hill et al., 2011). In animals, social structure is normally measured by factors such as the dominance gradient (the ability of low-ranking individuals to win fights with higher-ranking individuals), amount of social play, the intensity of aggression within populations and the frequency of conciliatory displays (Thierry et al., 2008). In species with a steep dominance gradient, social factors may hinder the invention and spread of cumulative modifications. A recent mathematical model of cultural progression found that increasing the number of tolerant knowledgeable individuals, is expected to generate higher levels of technological complexity, with tolerance thought to be essential in the initial stages of cultural progression (Pradhan et al., 2012). Thus, social structure may account for some variation in the extent of cumulative culture (Burkart & van Schaik, 2010; Coussi-Korbel & Fragaszy, 1995).

(i) Monopolisation: By monopolising resources and scrounging from low-rankers, dominant individuals may exploit those lower in the social hierarchy and prevent them from accessing novel resources (Lavallee, 1999; Soma & Hasegawa, 2004). In an experiment investigating tool use in free-ranging captive brown capuchins (*Cebus apella*), Lavallee (1999) reported that the alpha male would frequently chase low-ranking individuals away from the tree stump that contained resources of honey. Out of a group of 11 individuals, four never had the opportunity to interact with the task and others were also constrained in the amount of time they could spend at the resource. Similar findings have been reported in a study of social learning in wild lemurs (*Lemur catta*, Kendal et al., 2010a). In a review of the primate literature, Reader and Laland (2001) found that there were more reports of innovations in low-ranking individuals than high- or mid-ranking individuals. If low-ranking individuals have a greater propensity to innovate than high-ranking individuals but, because of the activities of dominants, experience restricted opportunities to interact with novel resources, or to perform any innovative behaviour they devise, then innovation may be curtailed. This, coupled with the reported decreased likelihood of individuals observing novel behaviour by low rankers compared to high rankers (Coussi-Korbel & Fragaszy, 1995; Kendal et al., In prep), means that the population may not be able to exhibit cumulative social learning.

(ii) Scrounging: Several studies have reported a relationship between the level of scrounging, or kleptoparasitism, that individuals commit and the amount that they learn socially (Giraldeau & Lefebvre, 1987; Beauchamp & Kacelnik, 1991; Lefebvre & Helder, 1997; Midford et al., 2000; Caldwell & Whiten, 2003),

although the direction of this relationship varies. Some studies have found that social learning was inhibited by scrounging (Giraldeau & Lefebvre, 1987; Lefebvre & Helder, 1997), leading to the hypothesis that, when able to scrounge, individuals do not learn cues about the task from the demonstrator, but rather learn that the demonstrator itself is a source of food (Giraldeau & Lefebvre, 1987; Beauchamp & Kacelnik, 1991). Scrounging, by inhibiting learning about the task itself, might therefore restrict the spread of social information, thereby hindering cumulative culture.

However, other researchers have found that scrounging enhanced the learning of observers regarding a novel extractive foraging puzzle box (Midford et al., 2000; Caldwell & Whiten, 2003). In these studies animals able to scrounge performed better when given the opportunity to interact with the novel task, than those that were not permitted to scrounge. The researchers argue that scrounging promoted closer observation of the novel behaviour pattern and attendance to cues of the puzzle box, rather than simply associating the demonstrator with food, which allowed the scrounger to learn a behaviour pattern more efficiently (Caldwell & Whiten, 2003).

Social learning may also depend upon species' social tolerance levels (Fragaszy & Visalberghi, 1989; Coussi-Korbel & Fragaszy, 1995; Caldwell & Whiten, 2003). Animals that display greater social tolerance of one another (more egalitarian species) may exhibit enhanced social learning with scrounging, since the co-action and close proximity allows the observers to learn from the demonstrator more effectively. In contrast, scrounging may have an inhibitory effect on social learning in despotic animals (displaying lower social tolerance) due to a reduction in the opportunity for coaction and subsequent ability of dominant individuals to access the resources (Coussi-Korbel & Fragaszy, 1995). An important contributing factor in the development of cumulative culture, thus, may be a species' level of social tolerance, with species displaying high social tolerance, such as *Homo sapiens*, able to transfer more complex information. However, since cumulative culture is not found in all egalitarian species, and a lack of social tolerance was not found to contribute to a lack of cumulative culture in chimpanzees or capuchins (Dean et al., 2012) factors other than social tolerance must also contribute to its evolution.

(d) Demography

Demographic factors have also been proposed to influence cumulative culture. Powell et al. (2009; 2010) have proposed that the changes in human culture during the late Pleistocene, observed in the archaeological record, are explained by demographic factors. Using simulation models building on a model of Henrich's (2004), Powell et al (2009; 2010) found that high population densities and high migration rates between subpopulations resulted in accumulation of modifications and increased complexity in technologies (see also Kline & Boyd, 2010). They hypothesise that population dynamics may have played an important part in the acceleration of cumulative cultural change around 50 kya. However, a key assumption of the models is the pre-existence of the cognitive capacities for social learning and cumulative culture in humans, therefore, clearly demography alone is insufficient to generate cumulative culture without these cognitive capabilities. Hill et al. (2011) highlight various hunter gatherer group composition properties unique among the primates that may have implications for the emergence of cumulative culture. These include hunter gatherer bands being composed of a large proportion of non-kin (suggesting cooperation between unrelated individuals), flexible patterns of male and/or female dispersal, maintained lifelong social bonds (Chapais, 2011; Rodseth et al., 1991) and bands forming constituent parts of larger social networks. A likely by-product of these group structures is pronounced social transmission and continued flow of cultural practices, knowledge and ideas between bands and sub-populations, accentuating the probability that traits will accumulate within and across populations. In contrast, for chimpanzees, (affiliative) contact between communities is composed almost exclusively of female migration, upon which contact with the natal group is lost (Chapais, 2011). Thus we see that human band compositions are especially well suited to cultural transmission on a large scale. As such, a species' demography may play an important role in whether or not their culture has accumulated over generations.

Enquist et al. (2010) investigated how the number of animals an individual is able to copy affects the persistence of a cultural trait over time. They used mathematical models to investigate under what conditions copying a single cultural 'parent' could support a stable culture. They found that multiple cultural parents were typically necessary for a stable culture as, unless perfect transmission was possible, then copying of single cultural parents would result in the proportion of individuals expressing a trait decreasing generation after generation. This suggests that a population with overlapping generations and the opportunity for learning from multiple individuals promotes cultural transmission.

Whilst a larger population size has a positive effect on the development and sustainability of complex cumulative culture, small, isolated populations may also lose cultural complexity. The best known example of cultural loss is the island of Tasmania, where humans arrived about 34 kya and were isolated from the mainland between 12 kya and 10 kya (Henrich, 2004). Subsequently, the Tasmanians lost all but 24 items in their toolkit, compared to a toolkit of hundreds on mainland Australia. Thus, when Europeans arrived in the 18th century there was no bone technology, no skills for making winter clothing and no ability to fish as seen in mainland Australian aborigine populations (Henrich, 2004). In modelling the data Henrich found that as population size dropped it became much easier for losses of behavioural traits to occur due to small copying errors. The isolation of Tasmania meant that the small population could rapidly lose technologies, with little chance of innovations from within their population or from migrant individuals.

The Tasmanian example is replicated with other populations in the Pacific Ocean. Kline and Boyd (2010) found that in Pacific islands the population size and rate of contact with other populations correlated with the complexity of the marine foraging technology. Whilst acknowledging that complex technologies may increase the carrying capacity of the population, the authors speculate that the influx of migrant ideas and range of ideas from a larger population allow modifications to cultural traits to be made more rapidly, ratcheting up complexity.

In summary, the size, network structure and mobility of populations may impact upon the number of cultural traits that a population can sustain. Clearly demography alone cannot account for the initial development of individual cumulative cultural traits, otherwise it would be widespread in nature. However, population size will influence the speed at which technologies ratchet up in complexity, and the level of diversity maintained (Pradhan et al., 2012).

(2) Efficiencies and complexities

Throughout this review, there has been discussion of empirical work and field observations that focus on an increase in complexity over time. The ratchet effect, as originally described by Tomasello (1994), specifically referred to increases in complexity with social transmission. This increase in complexity is hypothesised to have created the many artefacts, institutions and complex technologies that humans display across populations (Tomasello, 1999).

However, we wish to emphasise that in cumulative culture, combined with complexity, there must also be changes in efficiency. It is likely that cultural traits that simply become more complex, with no improvements in efficiency, would simply become too complex for individuals to learn or gain sufficient benefit to justify learning them. For example, Mesoudi (2011b) has posited a limit to cumulative complexity due to the costs of acquiring a complex trait from the previous generation within a life-time. An obvious example of the proposed requirement for improved efficiency alongside complexity is that of computing technology; computers, have become more compact, and user friendly, as they have become more powerful.

Some studies featured in this review have solely focussed on cumulative improvements in efficiency (Flynn, 2008; Kirby et al., 2008). Flynn (2008) finds that the imitation of causally irrelevant actions, (or ‘over-imitation’), as seen in other experiments with humans (Horner & Whiten, 2005; Nielsen & Tomaselli, 2010; Wood et al., 2012) reduces over laboratory generations with children employing rational rather than blind/faithful imitation, making the technique used to solve the task more efficient. Similarly, the decrease in diversity, and thus increase in efficiency, of Kirby et al.'s (2008) artificial languages, relies on mistakes made by individuals. Indeed, the structured manner in which individuals made language learning 'mistakes' resulted in the structure that emerged in the language, in turn enabling efficient language learning.

To take an alternative example, New Caledonian Crows are observed to make a variety of different hooked tools (Hunt & Grey, 2003). However, Sanz et al (2009) assert that these hooks do not enhance the efficiency with which the crows can gain food, they are simply additions to the tool which increase its physical complexity. We see this as an empirical issue: if evidence can be provided that step tools are more efficient than other tools then (provided these tools also meet the other criteria outlined in Table 1) they may yet prove to be a case of cumulative culture. Likewise, we may posit a similar argument for the stone-handling of Japanese macaques which may increase in complexity yet, as there is no apparent 'purpose' to the behaviour, does not increase efficiency. Finally, there are examples in human culture in which ceremonial or decorative items become more complex to manufacture, independent of their original function (functioning instead, for example, as signs of wealth, position, skill or power) and thus without increases in the efficiency with which a target is achieved (Basalla, 1988). For example, the Torres Strait culture created ornate decorative (turtle shell) fish hook ornaments that were worn by married women (Hedley, 1907, cited by Florek, 2005), creating complex, carved, symbolic cultural artefacts that did not increase the efficiency of the items' original fishing function (although the efficiency with which it acted as a display could be investigated).

We emphasise that whilst cumulative culture primarily drives the complexity of cultural traits, the efficiency with which the trait is transmitted, executed, and enables achievement of its intended purpose, may also change. Thus the interplay between the complexity and efficiency of cumulative cultural traits potentially influences how traits evolve with some showing increasing efficiency and reducing complexity (e.g. language change in the laboratory), some increasing complexity and increasing efficiency (e.g. computing technology) and others increasing in complexity and reducing in efficiency (e.g. symbolic culture). We believe that this is a neglected aspect of research into cumulative culture, which warrants further investigation.

VI. CONCLUSIONS

(i) Historical evidence suggests that human culture is cumulative, with successive generations building on what went before. This evidence is supported by empirical data, which suggests that humans are able to observe other individuals and modify what they have seen.

(ii) Although some researchers have argued that certain non-human species ratchet up the complexity of cultural traits, the evidence that non-humans have cumulative culture is weak. Presently there is no evidence that any species, except humans, have cumulative culture. Some evidence from the wild suggests that modifications have been made to the behavioural traits of some animals, but evidence that these were socially transmitted is lacking.

(iii) There have been a number of different hypotheses advanced for the evolution of cumulative culture. Current evidence supports the view that a package of sociocognitive capabilities (including teaching, imitation, verbal instruction and prosocial tendencies) present in humans, but not other animals, underpins cumulative cultural learning, probably because it promotes high-fidelity information transmission.

(iv) Currently, studies of cumulative culture often focus solely on increases in trait complexity. However, evidence from historical reports and experimental investigation suggest that there are also associated changes in trait efficiency, which warrant investigation.

Acknowledgements

LGD was supported by an EU-Nestpathfinder grant (043434FP6-2004-NESTPATH) to KNL, GV by a Durham University Social and Health Interdisciplinary Scholarship, KNL by an Advanced grant (EVOCULTURE 232823), EGF by an ESRC Grant, and RLK by a Royal Society Dorothy Hodgkin Fellowship. We appreciate helpful discussions with Jamie Tehrani, Jeremy Kendal and Tom Morgan.

(2005). So much more to know. — In: Science, p. 78-102.

Acerbi, A., Tennie, C. & Nunn, C. (2011). Modeling imitation and emulation in constrained search spaces. — Learning & Behavior 39, 104-114.

Asch, S. E. (1955). Opinions and Social Pressure. — Scientific American 193, 31-35.

Basalla, G. (1988). The Evolution of Technology. — Cambridge University Press, Cambridge.

Beauchamp, G. & Kacelnik, A. (1991). Effects of the knowledge of partners on learning rates in zebra finches *Taeniopygia guttata*. — Animal Behaviour 41, 247-253.

Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? — Evolutionary Anthropology 12, 82-91.

Boesch, C., Head, J. & Robbins, M. M. (2009). Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. — Journal of Human Evolution 56, 560-569.

Boyd, R. & Richerson, P. (1985). Culture and the Evolutionary Process. — Chicago University Press, Chicago.

Boyd, R. & Richerson, P. J. (1996). Why Culture is Common, but Cultural Evolution is Rare. — Proceedings of the British Academy 88, 77-93.

Burkart, J.M. & van Schaik, C.P. (2010). Cognitive consequences of cooperative breeding in primates? — Animal Cognition 13: 1-19

Caldwell, C. & Millen, A. (2008). Experimental models for testing hypotheses about cumulative cultural evolution. — Evolution and Human Behavior 29, 165-171.

Caldwell, C. A. & Millen, A. E. (2009). Social Learning Mechanism and Cumulative Cultural Evolution. — Psychological Science 20, 1478-1487.

—. (2010a). Conservatism in laboratory microsocieties: unpredictable payoffs accentuate group-specific traditions. — Evolution and Human Behavior 31, 123-130.

—. (2010b). Human cumulative culture in the laboratory: Effects of (micro) population size. — Learning and Behavior 38, 310-318.

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.

Caldwell, C. A. & Whiten, A. (2003). Scrounging faciliatates social learning in common marmosets, *Callithrix jacchus*. — Animal Behaviour 65, 1085-1092.

Caro, T. & Hauser, M. (1992). Is there teaching in nonhuman animals? — Quarterly Review of Biology 67, 151-174.

Carpenter, M. (2006). Instrumental, Social, and Shared Goals and Intentions in Imitation. — In: Imitation and the Social Mind. Autism and Typical Development (S. J. Rogers & J. H. G. Williams, eds). The Guilford Press, London.

Carpenter, M., Akhtar, N. & Tomasello, M. (1998). Fourteen- to 18-month old infants differentially imitate intentional and accidental actions. — Infant Behavior and Development 21, 315-330.

Cavalli-Sforza, L. & Feldman, M. (1981). Cultural Transmission and Evolution: A Quantitative Approach. — Princeton University Press, Princeton, NJ.

CHENEY, D. L. & SEYFARTH, R. M. (2010). Primate Communication and Human Language: Continuities and Discontinuities —In: Mind the Gap: Tracing the Origins of Human Universals (P. M. Kappeler & J. B. Silk, eds). Springer, Berlin.

COULTAS, J. C. (2004). When in Rome... And evolutionary perspective on conformity. — Processes & Intergroup Relations 7, 317-331.

COUSSI-KORBEL, S. & FRAGASZY, D. M. (1995). On the relation between social dynamics and social learning. — Animal Behaviour 50, 1441-1453.

CSIBRA, G. & GERGELY, G. (2005). Social learning and social cognition: The case for pedagogy. — In: Processes of Change in Brain and Cognitive Development. Attention and Performance (Y. Munakata & M. H. Johnson, eds). Oxford University Press, Oxford, p. 249-274.

D'ANDRADE, R. (2008). Some Kinds of Causal Powers That Make Up Culture. — In: Explaining Culture Scientifically (M. J. Brown, ed). University of Washington Press, 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.

DEREX, M., GODELLE, B. & RAYMOND, M. (2012). Social learners require process information to outperform individual learners. — Evolution, 67, 688-97.

EFFERSON, C., LALIVE, R., RICHERSON, P., MCELREATH, R. & LUBELL, M. (2008). Conformists and mavericks: the empirics of frequency-dependent cultural transmission. — Evolution and Human Behavior 29, 56-64.

EFFERSON, C., RICHERSON, P. J., MCELREATH, R., LUBELL, M., EDSTEN, E., WARING, T. M., PACIOTTI, B. & BAUM, W. (2007). Learning, productivity and noise: an experimental study of cultural tranmission on the Bolivian Altiplano. — Evolution and Human Behavior 28, 11-17.

EHN, M. & LALAND, K. N. (2012). Adaptive strategies for cumulative cultural learning. — Journal of Theoretical Biology 301, 103-111.

ENQUIST, M. & GHIRLANDA, S. (2007). Evolution of social learning does not explain the origin of human cumulative culture. — Journal of Theoretical Biology 246, 129-135.

ENQUIST, M., GHIRLANDA, S., JARRICK, A. & WACHTMEISTER, C.-A. (2008). Why does human culture increase exponentially? — Theoretical Population Biology 74, 46-55.

ENQUIST, M., STRIMLING, P., ERIKSSON, K., LALAND, K. & SJOSTRAND, J. (2010). One cultural parent makes no cultural —Animal Behaviour 79, 1353-1362.

ERIKSSON, K. & COULTAS, J. C. (2009). Are people really conformist-biased? An empirical test and a new mathematical model. — Journal of Evolutionary Psychology 7, 5-21.

ERIKSSON, K., ENQUIST, M. & GHIRLANDA, S. (2007). Critical points in current theory of conformist social learning. — Journal of Evolutionary Psychology 5, 67-87.

FLOREK, S. (2005). The Torres Strait Islands collection at the Australian Museum. -- Technical Reports of the Australian Museum 19, 1-19.

FLYNN, E. (2008). Investigating children as cultural magnets: do young children transmit redundant information along diffusion chains? — Philosophical Transactions of the Royal Society B: Biological Sciences 363, 3541-3551.

—. (2010). Underpinning Collaborative Learning. — In: Self and Social Regulation: Social interaction and the development of social understanding and executive functions (B. Sokol, U. Muller, J. Carpendale, A. Young & G. Iarocci, eds). Oxford University Press, Oxford, p. 312-336.

FOGARTY, L., STRIMLING, P. & LALAND, K. N. (2011). The evolution of teaching. — Evolution 65, 2760-2770.

FRAGASZY, D. M. & VISALBERGHI, E. (1989). Social influences on the acquistion and use of tools in tufted capuchin monkeys (*Cebus apella*). — Journal of Comparative Psychology 103, 159-170.

FRANKS, N. & RICHARDSON, T. (2006). Teaching in tandem-running ants. — Nature 439, 153-153.

GALEF, B. G. (1992). The Question of Animal Culture. — Human Nature 3, 157-178.

GALEF JR, B. G., DUDLEY, K. E. & WHISKIN, E. E. (2008). Social learning of food preferences in disatisfied and uncertain rats. — Animal behaviour 75, 631-637.

GERGELY, G., BEKKERING, H. & KIRALY, I. (2002). Rational imitation in preverbal infants. — Nature 415, 755.

GIRALDEAU, L. & LEFEBVRE, L. (1987). Scrounging prevents cultural transmission of food-finding behaviour in pigeons. — Animal Behaviour 35, 387-394.

GRUBER, T., MULLER, M. N., REYNOLDS, V., WRANGHAM, R. & ZUBERBUHLER, K. (2011). Community-specific evaluation of tool affordances in wild chimpanzees. — Sci. Rep. 1.

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.

HAUSER, M. D., CHOMSKY, N. & FITCH, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? — Science 298, 1569-1579.

HECHT, E. E., PATTERSON, R. & BARBEY, A. K. (2012). What can other animals tell us about human social cognition? An evolutionary perspective on reflective and reflexive processing. — Frontiers in Human Neuroscience 6.

HELFMAN, G. S. & SCHULTZ, E. T. (1984). Social traditions of behavioral traditions in a coral reef fish. — Animal Behaviour 32, 379-384.

HENRICH, J. (2004). Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: the Tasmanian case. — American Antiquity 69, 197-214.

HENRICH, J. & BOYD, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. — Evolution and Human Behavior 19, 215-241.

HERRMANN, E., CALL, J., HERNANDEZ-LLOREDA, M., HARE, B. & TOMASELLO, M. (2007). Humans Have Evolved Specialized Skills of Social Cognition: The Cultural Intelligence Hypothesis. — Science 317, 1360-1366.

HEYES, C. (1993). Imitation, culture and cognition. — Animal Behaviour 46, 999-1010.

HILL, K. R., WALKER, R. S., BOZICEVIC, M., EDER, J., HEADLAND, T., HEWLETT, B., HURTADO, A. M., MARLOWE, F., WIESSNER, P. & WOOD, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. — Science 331, 1286- 1289.

HOLZHAIDER, J. C., HUNT, G. R. & GRAY, R. D. (2010). Social Learning in New Caledonian crows. — Learning and Behavior 38, 206-219.

HOPPER, L. M. (2010). 'Ghost' experiments and the dissection of social learning in humans and animals. — Biological Reviews 85, 685-701.

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.

HOPPITT, W. J. E., BROWN, G. R., KENDAL, R., RENDELL, L., THORNTON, A., WEBSTER, M. M. & LALAND, K. N. (2008). Lessons from animal teaching. — Trends in Ecology & Evolution 23, 486-493.

HORNER, V. & WHITEN, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). — Animal Cognition 8, 164-181.

HORNER, V., WHITEN, A., FLYNN, E. & DE WAAL, F. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. — Proceedings of the National Academy of Sciences 103, 13878-13883.

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.

HUANG, C.-T. & CHARMAN, T. (2005). Gradations of emulation learning in infants imitation of actions on objects. — Journal of Experimental Child Psychology 92, 276-302.

HUFFMAN, M., NAHALLAGE, C. & LECA, J. (2008). Cultured Monkeys: Social Learning Cast in Stones. — Current Directions in Psychological Science 17, 410-414.

HUMLE, T. & MATSUZAWA, T. (2002). Ant-Dipping Among the Chimpanzees of Bossou, Guinea, and Some Comparisons With Other Sites. — American Journal of Primatology 58, 133-148.

HUNT, G. & GRAY, R. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. — Proceedings of the Royal Society B: Biological Sciences 270, 867-874.

—. (2004). The crafting of hook tools by wild New Caledonian crows. — Proceedings of the Royal Society B: Biological Sciences 271, S88-S90.

KANDLER, A. & LALAND, K. N. (2009). An investigation of the relationship between innovation and cultural diversity. — Theoretical Population Biology 76, 59-67.

KENDAL, J., RENDELL, L. R., PIKE, T. W. & LALAND, K. N. (2009a). Nine-spined sticklebacks employ a hill-climbing social learning strategy. — Behavioural Ecology 20, 238-244.

KENDAL, R., COE, R. & LALAND, K. (2005). Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. — American Journal of Primatology 66, 167-188.

KENDAL, R., KENDAL, J., HOPPITT, W. & LALAND, K. (2009b). Identifying Social Learning in Animal Populations: A New 'Option-Bias' Method. — PLoS One 4, e6541.

KENDAL, R. L., CUSTANCE, D. M., KENDAL, J. R., VALE, G., STOINKSI, T. S., RAKOTOMALALA, N. L. & RASAMIMANA, H. (2010a). Evidence for social learning in wild lemurs (*Lemur catta*). — Learning and Behavior 38, 220-234.

KENDAL, R. L., GALEF JR, B. G. & VAN SCHAIK, C. P., eds. (2010b). Capturing Social Learning in Natural Contexts: Methodological Insights and Implications for Culture. —.

KENDAL, R. L., HOPPER, L. M., BROSNAN, S. F., SCHAPIRO, S. J., LAMBETH, S. & HOPPITT, W. (In prep). Transmission biases in chimpanzees. —.

KENWARD, B., RUTZ, C., WEIR, A. A. S. & KACELNIK, A. (2006). Development of tool use in New Caledonian crows: inherited action patterns and social influence. — Animal Behaviour 72, 1329-1343.

KENWARD, B., WEIR, A. A. S., RUTZ, C. & KACELNIK, A. (2005). Tool manufacture by naive juvenile crows. — Nature 433, 121.

KIRBY, S., CORNISH, H. & SMITH, K. (2008). Cumulative Cultural Evolution in the Lab: an experimental approach to the origins of structure in human language. — Proceedings of the National Academy of Science 105, 10681-10686.

KLINE, M. A. & BOYD, R. (2010). Population size predicts technological complexity in Oceania. — Proceedings of the Royal Society B: Biological Sciences 277, 2559-2564.

KROEBER, A. L. & KLUCKHORN, C. (1952). Culture: A Critical Review of Concepts and Definitions. — Harvard University Press, Cambridge, MA.

LALAND, K. (2004). Social learning strategies. — Learning and Behavior 32, 4-14.

LALAND, K. N. & GALEF, B. G. (2009). The Question of Animal Culture. — Harvard University Press, Cambridge.

LALAND, K. N. & HOPPITT, W. (2003). Do animals have culture? — Evolutionary Anthropology 12, 150-159.

LALAND, K. N. & JANIK, V. M. (2006). The animal culture debate. — Trends in Ecology & Evolution 21, 542-547.

LALAND, K. N., KENDAL, J. R. & KENDAL, R. L. (2009). Animal Culture: Problems and Solutions. — In: The Question of Animal Culture (K. N. Laland & B. G. Galef, eds). Harvard University Press, Cambridge, Massachusetts, p. 174-197.

LAVALLEE, A. C. (1999). Capuchin (*Cebus apella*) tool use in a captive naturalistic environment. — International Journal of Primatology 20, 399-414.

LECA, J.-B., GUNST, N. & HUFFMAN, M. A. (2010). Indirect social influence in the maintenance of the stone-handling tradition in Japanese macaques, *Macaca fuscata*. — Animal Behaviour 79, 117-126.

LECA, J., GUNST, N. & HUFFMAN, M. (2007). Japanese macaque cultures: inter-and intra-troop behavioural variability of stone handling patterns across 10 troops. — Behaviour 144, 251-281.

LEFEBVRE, L. & HELDER, R. (1997). Scrounger numbers and the inhibition of social learning in pigeons. — Behavioural Processes 40, 201-207.

LEFEBVRE, L. & PALAMETA, B. (1988). Mechanisms, Ecology, And Population Diffusion of Socially-Learned Food-Finding Behaviour in Feral Pigeons. — In: Social Learning. Psychological and Biological Perspectives (T. Zentall & B. G. Galef, eds). Lawrence Erlbaum Associates, Hillsdale, NJ.

LEHMAN, H. (1947). The exponential increase of man's cultural output. — Social Forces, 281-290.

LEHNER, S. R., BURKHART, J. M. & VAN SCHAIK, C. P. (2011). Can captive orangutans (*Pongo pygmaeus abelli*) be coaxed into cumulative build-up of techniques? — Journal of Comparative Psychology 125, 446-455.

LEWIS, H. M. & LALAND, K. N. (In Press). Transmission fidelity is the key to the build-up of cumulative culture. — Philosophical Transactions of the Royal Society B.

LUMSDEN, C. J. & WILSON, E. O. (1981). Genes, Mind and Culture: The Coevolutionary Process. — Harvard University Press, Cambridge.

LYONS, D. E., DAMROSCH, D. H., LIN, J. K., MACRIS, D. M. & KEIL, F. C. (2011). The scope and limits of overimitation in the transmission of artefact culture. — Philosophical Transactions of the Royal Society B: Biological Sciences 366, 1158-1167.

LYONS, D. E., YOUNG, A. G. & KEIL, F. C. (2007). The hidden structure of overimitation. — Proceedings of the National Academy of Sciences 104, 19751-19756.

MARSHALL-PESCINI, S. & WHITEN, A. (2008). Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. — Animal Cognition 11, 449-456.

MATTHEWS, L. J., PAUKNER, A. & SUOMI, S. J. (2010). Can traditions emerge from the interaction of stimulus enhancement and reinforcement learning? An experimental model. — American Anthropologist 112, 257-269.

MCELREATH, R., BELL, A., EFFERSON, C., LUBELL, M., RICHERSON, P. & WARING, T. (2008). Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. — Philosophical Transactions of the Royal Society B: Biological Sciences 363, 3515-3528.

MCELREATH, R., LUBELL, M., RICHERSON, P., WARING, T., BAUM, W., EDSTEN, E., EFFERSON, C. & PACIOTTI, B. (2005). Applying evolutionary models to the laboratory study of social learning. — Evolution and Human Behavior 26, 483-508.

MERCADER, J., BARTON, H., GILLESPIE, J., HARRIS, J., KUHN, S., TYLER, R. & BOESCH, C. (2007). 4,300-Year-old chimpanzee sites and the origins of percussive stone technology. — Proceedings of the National Academy of Science 104, 3043-3048.

MESOUDI, A. (2011a). Variable Cultural Acquisition Costs Constrain Cumulative Cultural Evolution. — PLoS One 6, e18239.

—. (2011b). Variable cultural acquisition costs constrain cumulative cultural evolution. — PLoS ONE 6, e18239.

MESOUDI, A. & WHITEN, A. (2008). The multiple roles of cultural transmission experiments in understanding human cultural evolution. — Philosophical Transactions of the Royal Society B: Biological Sciences 363, 3489-3501.

MIDFORD, P. E., HAILMAN, J. P. & WOOLFENDEN, G. E. (2000). Social learning of a novel foraging patch in families of free-living Florida scrub-jays. — Animal Behaviour 59, 1199-1207.

MORGAN, T. J. H. & LALAND, K. N. (2012). The biological bases of conformity. — Frontiers in neuroscience 6, 87-87.

Morgan, T. J. H., Rendell, L. E., Ehn, M., Hoppitt, W. & Laland, K. N. (2012). The evolutionary basis of human social learning. — Proceedings of the Royal Society B: Biological Sciences 279, 653-662.

Nahallage, C. A. D. & Huffman, M. A. (2008). Comparison of Stone Handling Behavior in Two Macaque Species: Implications for the Role of Phylogeny and Environment in Primate Cultural Variation. — American Journal of Primatology 70, 1-9.

Nielsen, M. & Tomaselli, K. (2010). Overimitation in Kalahari Bushman Children and the Origins of Human Cultural Cognition. — Psychological Science 21, 729-736.

Overington, S. E., Morand-Ferron, J., Boogert, N. J. & Lefebvre, L. (2009). Technical innovations drive the relationship between innovativeness and residual brain size in birds. — Animal Behaviour 78, 1001-1010.

Panger, M., Perry, S., Rose, L., Gros-Louis, J., Vogel, E., Mackinnon, K. & Baker, M. (2002). Cross-site differences in foraging behavior of white-faced capuchins (*Cebus capucinus*). — American Journal of Physical Anthropology 119, 52-66.

Perry, S. (2008). Manipulative monkeys: the capuchins of Lomas Barbudal. —.

—. (2011). Social traditions and social learning in capuchin monkeys (Cebus). — Royal Society Philosophical Transactions Biological Sciences 366, 988-996.

Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., Mackinnon, K. C., Manson, J. H., Panger, M., Pyle, K. & Rose, L. (2003). Social conventions in wild white-faced capuchin monkeys: Evidence for traditions in a neotropical primate. — Current Anthropology 44.

Pike, T. W., Kendal, J., Rendell, L. R. & Laland, K. N. (2010). Learning by proportional imitation in a species of fish. — Behavioural Ecology 21, 570-575.

Pinker, S. & Jackendoff, R. (2005). The faculty of language: what's special about it? — Cognition 95, 201-236.

Powell, A., Shennan, S. J. & Thomas, M. G. (2009). Late Pleistocene demography and the appearance of modern human behavior. — Science 324, 1298-1301.

—. (2010). Demography and Variation in the Accumulation of Culturally Inheritied Skills. — In: Innovation in Cultural Systems. Contributions from Evolutionary Anthropology (M. J. O'Brien & S. J. Shennan, eds). MIT Press, London, p. 137-160.

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.

Premack, D. (2007). Human and animal cognition: Continuity and discontinuity. — Proceedings of the National Academy of Sciences 104, 13861.

Price, E. E., Lambeth, S. P., Schapiro, S. J. & Whiten, A. (2009). A potent effect of observational learning on chimpanzee tool construction. — Proceedings of the Royal Society B: Biological Sciences 276, 3377-3383.

Raihani, N. J. & Ridley, A. R. (2008). Experimental evidence for teaching in wild pied babblers. — Animal Behaviour 75, 3-11.

Reader, S. & Laland, K. (2001). Primate innovation: sex, age and social rank differences. — International Journal of Primatology 22, 787-805.

—. (2002). Social intelligence, innovation, and enhanced brain size in primates. — Proceedings of the National Academy of Sciences 99, 4436.

Reader, S. M. & Biro, D. (2010). Experimental identification of social learning in wild animals. — Learning and Behavior 38, 265-283.

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T. & Laland, K. N. (2010). Why copy others? Insights from the social learning tournament. — Science 328, 208-213.

Richerson, P. & Boyd, R. (2005). Not by Genes Alone: How culture transformed human evolution. — University of Chicago Press, Chicago.

Sanz, C. & Morgan, D. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. — Journal of Human Evolution 52, 420-433.

—. (2009). Flexible and Persistent Tool-using Strategies in Honey-gathering by Wild Chimpanzees. — International Journal of Primatology 30, 411-427.

Sanz, C. M., Schoning, C. & Morgan, D. B. (2009). Chimpanzees Prey on Army Ants with Specialized Tool Set. — American Journal of Primatology 71, 1-8.

Schlag, K. H. (1998). Why Imitate, and If So, How?: A Bounded Rational Approach to Multi Armed Bandits. — Journal of Economic Theory 78, 130-156.

Seed, A., Clayton, N. & Emery, N. (2007). Postconflict third-party affiliation in rooks, Corvus frugilegus. — Current Biology 17, 152-158.

Soma, M. & Hasegawa, T. (2004). The effect of social facilitation and social dominance on foraging success of budgerigars in an unfamiliar environment. — Behaviour 141, 1121-1134.

Sterelny, K. (2009). Peacekeeping in the Culture Wars. — In: The Question of Animal Culture (K. N. Laland & B. G. Galef, eds). Harvard University Press, Cambridge.

Sugiyama, Y. (1997). Social tradition and the use of tool-composites by wild chimpanzees. — Evolutionary Anthropology 6, 23-27.

Tennie, C., Call, J. & Tomasello, M. (2009). Ratcheting Up the Ratchet: On the Evolution of Cumulative Culture. — Philosophical Transactions of the Royal Society Series B 364, 2405.

—. (2012). Untrained Chimpanzees <italic>(Pan troglodytes schweinfurthii)</italic> Fail to Imitate Novel Actions. — PLoS ONE 7, e41548.

Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C. & de Waal, F. B. M. (2008). A comparative study of conflict resolution in macaques: insights into the nature of trait covariaion. — Animal Behaviour 75, 847-860.

Thornton, A. & McAuliffe, K. (2006). Teaching in wild meerkats. — Science 313, 227-229.

Tomasello, M. (1994). The question of chimpanzee culture. — In: Chimpanzee Cultures (R. W. Wrangham, W. C. McGrew, F. B. M. de Waal & P. G. Heltne, eds). Harvard University Press, Cambridge, MA, p. 301-377.

—. (1999). The Cultural Origins of Human Cognition. — Harvard University Press, London.

Tomasello, M. & Call, J. (1997). Primate Cognition. — Oxford University Press, Oxford.

Tomasello, M. & Carpenter, M. (2007). Shared Intentionality. — Developmental Science 10, 121-125.

Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. — Behavioral and Brain Sciences 28, 675-735.

Tomasello, M., Kruger, A. C. & Ratner, H. H. (1993). Cultural Learning. — Behavioral and Brain Sciences 16, 495-552.

Tomasello, M. & Moll, H. (2010). The Gap is Social: Human Shared Intentionality and Culture. — In: Mind the Gap. Tracing the Origins of Human Universals (P. M. Kappeler & J. B. Silk, eds). Springer, Berlin.

van der Post, D. & Hogeweg, P. (2008). Diet traditions and cumulative cultural processes as side-effects of grouping. — Animal Behaviour 75, 133-144.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. — Science 299, 102-105.

Warner, R. R. (1988). Traditionality of mating-site preferences in a coral reef fish. — Nature 335, 719-721.

Whiten, A., Custance, D., Gomez, J., Teixidor, P. & Bard, K. (1996). Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). — Journal of Comparative Psychology 110, 3-14.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. (1999). Cultures in chimpanzees. — Nature 399, 682-685.

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

Whiten, A., McGuigan, N., Marshall-Pescini, S. & Hopper, L. (2009). Emulation, Imitation, Overimitation and the Scope of Culture for Child and Chimpanzee —Philosophical Transactions of the Royal Society B: Biological Sciences 364, 2417-2428.

Whiten, A. & van Schaik, C. (2007). The evolution of animal 'cultures' and social intelligence. — Philosophical Transactions of the Royal Society B: Biological Sciences 362, 603-620.

Wisdom, T. N. & Goldstone, R. L. (2010). Social learning and cumulative mutual improvement in a networked group. — In: Proceedings of the 32nd Annual Conference of the Cognitive Science Society (S. Ohlsson & R. Catrambone, eds), Austin, TX, p. 1405-1410.

Wood, L., Kendal, R. L. & Flynn, E. (2012). Context dependent model-based biases in cultural transmission: Children's imitation is affected by model age over model knowledge state. — Evolution and Human Behavior 104, 367-381.

Wood, L.A., Kendal, R.L. & Flynn, E.G. (2013) Copy me or copy you? The effect of prior experience on social learning. Cognition, 127: 203-213

Ziman, J. (2000). Real Science: What it is and what it means. — Cambridge University Press, Cambridge.