

Human cumulative culture: a comparative perspective

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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, orangutans 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 processes of cumulative culture and emphasising areas of agreement and disagreement amongst investigators in separate fields.

Key words: cumulative culture, cultural evolution, ratcheting, social learning, animal traditions.

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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, 2007; Mesoudi, 2011), 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 (Anon., 2005) list of 125 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.

Herein 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, and 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 11000 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, p. 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 & Hoppitt (2003, p. 151), we define culture as ‘group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information’. This established, we now consider what is known about culture in non-human animals.

(2) The animal culture 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 & 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 & 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 & van Schaik (2007) restrict culture to those species with traditions in at least two different behavioural domains, specifically chimpanzees (*Pan troglodytes*), orangutans (*Pongo* spp.) 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.2a). Thus, although Whiten & 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, Kendal & Kendal, 2009; Kendal, Galef & van Schaik, 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. Comparative psychologist Michael Tomasello 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, Kruger & Ratner, 1993; Tomasello, 1994, 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, 2012). Pradhan, Tennie & van Schaik (2012) 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, Call & Tomasello, 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, or 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) 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, and 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 (1947) demonstrated exponential growth in these fields on an historical timescale (from 1000 to 1600 AD through to the 20th Century). Although Lehman’s (1947) data may be somewhat subjective, he used multiple sources for the definition of an ‘outstanding contribution’ in a particular field. He illustrates that by building upon previous knowledge, humans 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) did 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) Empirical research

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, Cornish & Smith (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 (2008) 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 was provided by Caldwell & Millen (2008,

2010*b*). Experimental micro-populations were set simple tasks, such as making paper aeroplanes 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, 2010*a*). 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 5 min 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 & Millen (2009) applied the transmission chain design to examine the mechanisms underlying cumulative changes in cultural traits, in this case making paper aeroplanes. 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 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 (2003) believes this is an elaboration of an ancestral behaviour pattern of hitting nuts on the substratum to smash them. This behaviour pattern has, according to Boesch (2003), 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 that chimpanzee nut-cracking stone technology could date as far back as 4300 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

Table 1. Summary and assessment of field observations of proposed cumulative culture in non-human animal species

Species	Description of study	Evidence of cultural trait		Evidence of cumulative cultural trait		
		Evidence of initial innovation	Evidence of social learning within a generation	Evidence of social learning between generations	Trait moves beyond individual innovation capacity	Modification from a different domain
<i>Pan troglodytes</i>	Observations of different nut-cracking traditions in wild populations across Africa ^a	× Original innovation not observed	? Trait observed in multiple individuals. Mechanism of transmission not tested	? Trait observed in multiple generations. Circumstantial evidence of social learning	× No evidence that one individual could not have invented whole trait alone	×
	Different traditions for handling parasites across three populations ^a	× Original innovations not observed	? Trait observed in multiple individuals. Mechanism of transmission not tested	? Trait observed in multiple generations. Mechanism of transmission not tested	× No evidence that one trait is ancestral to others. Trait within-individual innovation capacity	×
	In arid conditions, wells dug near contaminated water. Wells combined with leaf-sponges ^a	× Original innovation not observed	? Trait observed in multiple individuals. Mechanism of transmission not tested	× Unclear if trait transmitted between generations. Mechanism of transmission not tested	× No evidence that one trait is ancestral to others. Trait within-individual innovation capacity	?
	Multiple tools to hunt invertebrates observed in some west African populations ^{b-d}	× Original innovation not observed	? Trait observed in multiple individuals. Mechanism of transmission not tested	× Unclear if trait transmitted between generations. Mechanism of transmission not tested	? Circumstantial evidence that single tool set pre-dates multiple tool set	×
<i>Cebus</i> spp.	The invention and diffusion of three social games observed in a single population. ^e	✓ Evidence that single individual produced multiple modifications	? Trait observed in multiple individuals. Likely to be passed on by social learning	× Games transient and disappeared relatively quickly after invention	× One individual appears to have invented all games alone	×
<i>Macaca fuscata</i>	Stone-handling traditions vary across Japan ^{f-h}	? New traits have emerged over time	? Traits observed in multiple individuals. Likely to be passed on by social learning	? Stone-handling behaviour has persisted over multiple generations, although trait types have changed	× No evidence that one individual could not have invented each trait alone	×
<i>Corvus moneduloides</i>	<i>Pandanus</i> tools vary in design across New Caledonia ^{i,j}	× Original innovation not observed	? Trait observed in multiple individuals	? Trait observed in multiple generations. Circumstantial evidence of social learning	× No evidence that one individual could not have invented each trait alone	×

^aBoesch (2003).^bSanz & Morgan (2007).^cSanz & Morgan (2009).^dBoesch *et al.* (2009).^ePerry *et al.* (2003).^fLeca *et al.* (2007).^gLeca *et al.* (2010).^hHuffman *et al.* (2008).ⁱHunt & Gray (2003).^jHolzhaider *et al.* (2010).

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, Head & Robbins, 2009; Sanz & Morgan, 2009; Sanz, Schoning & Morgan, 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 sets 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. These 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 characterised 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 occasionally to occur concurrent with the 'hand sniff' (Perry & Manson, 2008), representing conjunction of the two conventions. Importantly however, this eye-poke convention, along with the other reported social conventions, seems 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 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 characterised better 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, Gunst & Huffman, 2007, 2010; Huffman, Nahallage & Leca, 2008; Nahallage & Huffman, 2008). 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 unambiguous improvements. If these traits are non-adaptive, as it is claimed (Leca *et al.*, 2007), then there would seem to be little reason for 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 *Corvus moneduloides* (Hunt & Gray, 2004; Seed, Clayton & Emery, 2007). The species uses several tools, the most studied of which are constructed from *Pandanus* leaves, which are used for foraging. Hunt & 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 & Gray (2003) propose that the wide tools are ancestral 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 that 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, Hunt & Gray, 2010) and evidence from captivity indicates that New Caledonian crows may possess an inherited predisposition for tool use and tool manipulation (Kenward *et al.*, 2005, 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.

(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 2 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, Preuschoft & van Schaik, 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 it. 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 suggesting that they 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, these authors 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. 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 h of presentation of the task to each of four chimpanzee groups, only 1 of 33 individuals reached stage 3, with a further four 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 h, 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 h), 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.* (2012) 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.

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 localised traditions, animal cultures are either not cumulative at all or cumulative in a highly restricted and simple manner.

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. These data suggest 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.*, submitted).

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, Kendal & Flynn (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, Burkhardt & van Schaik (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, 2012). 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, Paukner & Suomi, 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 that few hard data exist here), then Lewis & Laland's (2012) 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, Tennie & Nunn, 2011; Derex, Godelle & Raymond, 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, Call & Tomasello, 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, Patterson & Barbey, 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, Young & Keil, 2007; Lyons *et al.*, 2011)].

(iv) *Adaptive filtering.* Enquist & 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, Akhtar & Tomasello, 1998; Gergely, Bekkering & Kiraly, 2002) or reliable learning heuristics (Laland, 2004) dictating what (and whom, e.g. Wood, Kendal & Flynn, 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 (*Suricata suricatta*), pied babblers (*Turdoides bicolor*), ants (*Temnothorax albipennis*) and bees (*Apis* spp) (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 characterised as behaviour that functions specifically to enhance the fidelity of information transmission. A recent mathematical analysis of the evolution of teaching (Fogarty, Strimling & Laland, 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, Chomsky & Fitch, 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 from 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 hypothesised 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, Coe & Laland, 2005; Kendal *et al.*, 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, Horner & De Waal, 2005). Our definition of conformity differs from that deployed in social psychology, which focusses 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 wide range of conditions (Henrich & Boyd, 1998) and contributes to the high-fidelity transmission required for cumulative culture. However, Eriksson, Enquist & Ghirlanda (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 (2007) 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, Rekers & Tomasello, 2012). Specifically, after observing three conspecifics demonstrating the same behaviour (each dropping a ball into a coloured box) or one individual demonstrating a different behaviour three times (dropping a ball three times into a different coloured box), chimpanzees and children copied the behaviour of the majority. By 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, interpretation of these data is open to debate (T. Morgan, personal communication). As noted by Haun *et al.* (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 (T. Morgan, personal communication). Further data will help clarify majority-biased learning in these species.

Kandler & 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 (Coultras, 2004; McElreath *et al.*, 2005, 2008; Efferson *et al.*, 2007, 2008; Eriksson & Coultras, 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 & Laland (2012) 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 & Goldstone (2010) recently demonstrated this sensitivity to the performance of others in the laboratory by exposing human participants to a computerised 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 non-human animals is currently limited to a handful of studies. Galef, Dudley & Whiskin (2008) reported evidence for a ‘proportional reservation’ strategy, as set out by Schlag (1998), in female Norway rats (*Rattus norvegicus*). Rats exposed to energetically dilute diets displayed a greater propensity to copy the food choices of demonstrator rats than did 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.*, 2009b).

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 these 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, Shennan & Thomas, 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 (Coussi-Korbel & Fragaszy, 1995; Burkart & van Schaik, 2010).

(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 a tree stump that contained resources of honey. Out of a group of 11 individuals, 4 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 & Laland (2001) found that there were more reports of innovations in low-ranking individuals than in 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.*, submitted), 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, Hailman & Woolfenden, 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. By 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 co-action 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) 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 50000 years ago (kya). However, a key assumption of the models is the pre-existence of 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 (Rodseth *et al.*, 1991; Chapais, 2011) 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. By 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 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 (2004) 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 & 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 (2011) posited a limit to cumulative complexity due to the costs of acquiring a complex trait from the previous generation within a lifetime. 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 & Gray, 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, do not increase in 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 Islanders 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 item’s 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 complexity and reducing efficiency (e.g. symbolic culture). We believe that this is a neglected aspect of research into cumulative culture, which warrants further investigation.

VI. CONCLUSIONS

(1) 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.

(2) 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.

(3) 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 absent or present to a lesser extent in other animals, underpins cumulative cultural learning, probably because it promotes high-fidelity information transmission.

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

VII. ACKNOWLEDGEMENTS

L.G.D. was supported by an EU-Nestpathfinder grant (043434FP6-2004-NESTPATH) to K.N.L., G.V. by a Durham University Social and Health Interdisciplinary Scholarship, K.N.L. by an Advanced grant (EVOCULTURE 232823), E.G.F. by an ESRC Grant, and R.L.K. by a Royal Society Dorothy Hodgkin Fellowship. We appreciate helpful discussions with Jamie Tehrani, Jeremy Kendal and Tom Morgan. We are grateful for the helpful comments of an anonymous reviewer and Claudio Tennie.

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(Received 24 June 2012; revised 24 June 2012; accepted 30 July 2013)