

Review

Studying cumulative cultural evolution in the laboratory

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Cumulative cultural evolution is the term given to a particular kind of social learning, which allows for the accumulation of modifications over time, involving a ratchet-like effect where successful modifications are maintained until they can be improved upon. There has been great interest in the topic of cumulative cultural evolution from researchers from a wide variety of disciplines, but until recently there were no experimental studies of this phenomenon. Here, we describe our motivations for developing experimental methods for studying cumulative cultural evolution and review the results we have obtained using these techniques. The results that we describe have provided insights into understanding the outcomes of cultural processes at the population level. Our experiments show that cumulative cultural evolution can result in adaptive complexity in behaviour and can also produce convergence in behaviour. These findings lend support to ideas that some behaviours commonly attributed to natural selection and innate tendencies could in fact be shaped by cultural processes.

Keywords: culture; cumulative cultural evolution; ratchet effect; social learning

1. BACKGROUND

In this review, we aim to explain why there is currently a need for an experimental science of cumulative cultural evolution. We will discuss methods that we have developed, which we believe can be employed in order to test experimental hypotheses about cumulative cultural evolution. We will also discuss the results that we have obtained using these methods and the implications that these findings have for our understanding of the effects of cumulative cultural evolution on human behaviour.

(a) *What is cumulative cultural evolution?*

In order to explain the motivation behind our research on cumulative cultural evolution, we begin by explaining why it is an interesting behavioural phenomenon and an important topic of study. Cumulative cultural evolution is distinct from culture in the general sense in a number of ways. While culture is accepted by most to refer to a socially transmitted heritage peculiar to a particular society (Boyd & Richerson 1985),¹ the definition of cumulative cultural evolution is considerably narrower. Boyd & Richerson (1994) showed that social learning could increase the average fitness of a population if it permitted ‘learned improvements to accumulate from one generation to the next’ (p. 134), essentially describing what they later termed cumulative cultural evolution (Boyd & Richerson 1996). Tomasello (1990, 1999; Tomasello *et al.* 1993) has coined the term ‘the ratchet effect’ to capture a similar notion: ‘The process of cumulative cultural evolution requires not

only creative invention but also, and just as importantly, faithful social transmission that can work as a ratchet to prevent slippage backward—so that the newly invented artifact or practice preserves its new and improved form at least somewhat faithfully until a further modification or improvement comes along.’ (Tomasello 1999, p. 5). Hence, cumulative cultural evolution refers to situations in which social transmission allows for successive improvements to performance over generations of learners, generated by the accumulation of modifications to the transmitted behaviours.

Cumulative cultural evolution in this sense should be distinguished from cultural evolution that does not lead to appreciable improvement in the efficiency of the behaviours in question. Mesoudi *et al.* (2004) have argued that all human culture constitutes an evolutionary process, since it involves variation (multiple traits that may be copied), heritability (similarity between traits as a result of copying) and competition (some traits are copied more than others), leading to the accumulation of modifications over time. However, not all such examples involve increasing efficiency or complexity. They therefore do not constitute the kind of learning that Boyd & Richerson (1994) or Tomasello (1999) were referring to, whereby each generation is provided with short cuts to the end results of extensive trial and error learning amassed by their cultural ancestors. So, although methods developed in evolutionary biology are currently proving extremely useful in reconstructing the history of cultural products, such as textile designs (Tehrani & Collard 2002), linguistic forms (Gray & Jordan 2000) and stories (Barbrook *et al.* 1998), these examples do not represent the kind of process that we are referring to as cumulative cultural evolution.

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One contribution of 11 to a Theme Issue ‘Cultural transmission and the evolution of human behaviour’.

All the same, even in these narrow terms, cumulative cultural evolution seems to pervade human society. Each generation builds on the knowledge, inventions and achievements of the previous one. Our present-day technologies exist only as a result of our ability to understand and make use of the imparted knowledge and artefacts of others. By contrast, the phenomenon of cumulative cultural evolution seems to be intriguingly rare in non-humans. This is despite the fact that there are plenty of cases of animal culture in the more general sense. To take just one well-known example, the sweet potato washing behaviour of the Japanese macaques of Koshima (e.g. Kawamura 1959; Kawai 1965) appears to have been acquired through social learning, since the behaviour spread initially to the close associates of the first monkey to use this technique, and then on to those individuals' associates. However, as a number of researchers have pointed out (most notably Boyd & Richerson 1996), examples of animal social learning such as this typically involve relatively simple behaviours that could also be readily learned through individual trial and error processes. There is little evidence of successive improvement over generations, or of the accumulation of modifications, and therefore no suggestion that the behaviours concerned could not have been invented by a single individual.

(b) *Debates in cumulative cultural evolution*

A strong motivation for us in developing experimental methods for studying cumulative cultural evolution was the fact that there are a number of important unresolved issues surrounding this topic, which have been the focus of much debate. The issue of whether cumulative cultural evolution is unique to humans, or merely relatively rare in non-humans, is just one of these. In addition, there is still disagreement over the learning mechanisms upon which cumulative cultural evolution may depend, and also the extent to which it is responsible for complex adaptive human behaviours. The details of these debates are summarized below.

(i) *Human uniqueness*

The question that has probably drawn the most attention surrounding cumulative cultural evolution is that of whether the phenomenon is unique to humans. As noted above, Boyd & Richerson (1996), among others, have drawn attention to the fact that although social learning is relatively common in the animal kingdom, cumulative cultural evolution appears to be extremely rare: 'cumulative cultural evolution resulting in behaviors that no individual could invent on their own is limited to humans, song birds, and perhaps chimpanzees' (Boyd & Richerson 1996, p. 77). Likewise, Heyes (1993) has drawn a distinction between the sorts of behaviours that non-humans appear to learn socially, in comparison with those of humans: 'the human attributes that are described as 'cultural' in ordinary discourse, seem to be a good deal more complex than, for example, potato washing and termite-fishing...and it is plausible that their greater complexity derives from the accumulation of modifications' (Heyes 1993, p. 1004).

Even stronger statements have been made by others. For example, Galef (1992) has stated that 'human culture accumulates over generations and can lead to

invention and transmission of increasingly complex behaviours. No one has claimed that any animal learns any behaviour from conspecifics that it could not learn independently through interaction with its physical environment' (Galef 1992, p. 161). Along similar lines, Tomasello (1999) has asserted that 'the cultural traditions and artifacts of human beings accumulate modifications over time in a way that those of other animal species do not' (Tomasello 1999, p. 5).

Of course, these authors are not claiming that social learning does not help animals to acquire useful behaviours. The example of the Koshima macaques illustrates how an advantageous invention can readily spread through a group. The issue is again the notion of the cultural ratchet, and of later generations exploiting the labours of previous ones in a way that allows them to make use of behaviours that they could not have learned by themselves.

All the same, some researchers have argued that there is in fact compelling evidence for cumulative cultural evolution in non-humans. For example, Boesch (2003) cited three examples of chimpanzee behaviours that he suggests may have arisen through accumulated modifications of socially learned behaviour. One of these is nut-cracking behaviour, which is observed in West African chimpanzee populations (Whiten *et al.* 1999). While some chimpanzees use fixed anvils, such as tree roots, others use loose stones. Furthermore, Sugiyama (1997) reported that some chimpanzees at the Bossou field site sometimes used an extra stone to stabilize the stone anvils upon which the nut is placed for cracking, perhaps indicating a refinement of the simpler technique.

Whiten *et al.* (2003) have put forward similar examples of possible cumulative culture in chimpanzees, including the above-mentioned nut-cracking behaviour. They also suggested that the alternative tool-use techniques used to forage on ants could show evidence of ratcheting. Of the two methods used, one is more elaborate, involving bimanual coordination, and also results in a greater yield (Humble & Matsuzawa 2002) and therefore Whiten *et al.* (2003) suggested that this could represent an elaboration on the simpler version.

Cumulative culture has also been proposed in species other than chimpanzees. Hunt & Gray (2003) proposed that the tool manufacture skills observed in New Caledonian crows had been acquired through cumulative cultural evolution. They were able to document population-specific methods of tool manufacture, which were apparently unrelated to local ecological conditions, and these different methods showed varying degrees of complexity. They therefore argued that these different techniques had been developed through cumulative cultural evolution. However, it is still unclear whether these techniques are socially learned at all, as it seems that tool manufacture abilities may be largely under genetic control in this species (Kenward *et al.* 2005).

There is clearly good reason to remain open-minded with regard to the question of whether cumulative cultural evolution is unique to humans. Boesch & Tomasello (1998), for example, have made the point that we have very little data on the behaviour of previous generations of chimpanzees, since long-term

studies of their behaviour began only *ca* 40 years ago. This inevitably makes it difficult to judge whether their behaviour has shown any ratcheting over time.

(ii) *The cognitive underpinnings of cumulative cultural evolution*

Related to the above debate, researchers have also deliberated over the issue of the cognitive mechanisms that may or may not be necessary for cumulative culture. This is necessarily tied in with the issue of which species exhibit this phenomenon, since beliefs about which cognitive processes may be involved have typically lain behind opinions about which species possess the capacity.

For example, [Boyd & Richerson \(1996\)](#) have made a compelling argument that a capacity for 'true imitation' is necessary for cumulative cultural evolution. By true imitation they refer to any form of learning in which individuals can learn a new behaviour by perceiving another individual's performance of that behaviour. [Boyd & Richerson \(1996\)](#) also used the term 'observational learning', which may be slightly misleading in this context as visual perception is not necessarily involved, since their definition encompasses learning about vocal communication, such as the learning of grammatical rules ([Richerson & Boyd 2005](#)) and bird song learning. In any case, other types of social learning, which they specify *cannot* support cumulative cultural evolution, are those in which the behaviour itself is not what is learned from another individual. Similar behaviours may arise between two individuals because the actions of one individual function to draw the attention of another to a particular location ('local enhancement') or class of objects ('stimulus enhancement'; [Whiten & Ham 1992](#)). However, in such cases, the behaviour is learned by trial and error, and the presence of the other individual has simply made that learning more likely.

[Boyd & Richerson \(1996\)](#) argued that, since cumulative cultural evolution by definition must allow learners to proceed from a more advanced starting point than was possible for previous generations, true imitation is a necessary condition for its occurrence. Learning that relies upon trial and error processes will inevitably mean that each new learner has to start from scratch, thereby wiping out any useful innovations that may have been chanced upon by others.

[Tomasello](#) (e.g. [Tomasello et al. 1993](#); [Tomasello 1999](#)) has made a similar argument, proposing that imitation and teaching, each dependent on a capacity for taking the perspective of another, are the foundations of cumulative cultural evolution. Like [Boyd & Richerson](#), [Tomasello](#) has not only stressed the importance of faithful transmission (and therefore imitation) but has also emphasized the need for an understanding of the goals of other individuals. Understanding what cultural practices are *about*, such as what a tool is used for, or what a particular communicative signal means, is crucial to human cultural learning ([Tomasello 1999](#)), so he has suggested this to be another necessary feature of cumulative cultural evolution (see also [Hermann et al. \(2007\)](#) for a recent conceptualization of this view).

However, not all theorists see things in this way. [Heyes \(1993\)](#), for example, has stated that there is no reason why imitation should be particularly crucial to the generation of cumulative behavioural change. [Heyes \(1993\)](#) proposed that the particular learning mechanism involved is in fact irrelevant to the issue of faithful transmission, and that what really matters is whether or not a behaviour will extinguish once learned. [Heyes \(1993\)](#) cited [Galef et al.'s \(1986\)](#) data from a two-action study on budgerigars: subjects that observed conspecifics accessing hidden food using either their beak or their foot tended to match the demonstrated technique for only the first two trials post demonstration. In later trials, the difference between the groups disappeared. Therefore, she has argued that behaviours learned via imitation, like any other, will be subject to modification from trial and error learning. [Heyes \(1993\)](#) proposed that in fact cumulative culture would be more likely to be supported by a separate insulating mechanism that protects socially learned information against the influence of trial and error learning.

[Laland & Hoppitt \(2003\)](#), similarly, have argued that there is currently no reason to believe that either imitation or teaching is particularly significant to cumulative cultural evolution. [Laland \(2004\)](#) has instead suggested that an ability to evaluate the relative effectiveness of behavioural alternatives would be a more plausible cognitive precursor to cumulative culture. Along similar lines, [Enquist & Ghirlanda \(2007\)](#) have argued for the importance of an 'adaptive filtering' mechanism. Modelling populations of social learners, [Enquist & Ghirlanda \(2007\)](#) concluded that, without such a filter, cumulative culture would result in the acquisition of many maladaptive traits and therefore could not evolve. However, a capacity to filter out maladaptive traits causes adaptive traits to accumulate preferentially, generating the ratchet effect that is characteristic of human culture.

In conclusion, therefore, there are a range of different views regarding the cognitive abilities upon which cumulative cultural evolution may depend. However, experimental work on this topic could contribute greatly to addressing this question, as we hope to elucidate later, and such work will also have implications for questions about human uniqueness.

(iii) *The origins of complex human behaviour*

Just as there is disagreement over the precursors to cumulative cultural evolution, as detailed above, there are also conflicting views on the outcomes of this process, which we will outline here. There is broad agreement that cumulative cultural evolution is responsible for a number of particularly interesting human traits. Indeed, this goes some way to explaining why so many researchers have been fascinated by this phenomenon. [Tomasello](#) (e.g. 1999) has argued that, given that our species shared a common ancestor with chimpanzees a mere 6 million years ago, the cognitive achievements of modern humans (such as written language, mathematics and complex technologies) have developed implausibly rapidly to be attributed to natural selection on behaviour. Instead he has proposed that cumulative cultural evolution may have played a significant role, and that this would have

allowed for much more rapid behavioural change than would genetic evolution. Boyd & Richerson (1996) have emphasized the influence of cumulative cultural evolution in terms of the success of humans as a species. Our ability to exploit a range of habitats has allowed us to become the most widespread animal on the planet.

However, recently, arguments have been put forward which propose a role for cumulative cultural evolution in the origins of behaviours that have been popularly believed to be largely dependent on naturally selected innate tendencies. For example, the structural properties shared by many different languages (usually referred to as linguistic universals) have often been argued to be good evidence of innate language-specific capabilities, common to all humans (e.g. Pinker & Bloom 1990). However, this view has recently been challenged by Kirby *et al.* (2007) and Christiansen & Chater (*in press*), among others (see also Smith & Kirby 2008).

Kirby *et al.* (2007) have argued that even extremely weak biases in learning (such as an expectation of regularity) can, over generations of learners, result in languages that are strongly adapted to those biases. The result of this is that no language-specific capacity is necessary in order to explain the existence of linguistic universals, as universals could arise from slight biases in general-purpose learning mechanisms. Within this view, languages are therefore seen as shaped by the brain (Christiansen & Chater *in press*) through the repeated cycle of learning and use over many generations, rather than the brain being adapted to language.

The crucial question here really is whether cumulative cultural evolution, driven by general learning mechanisms, can account for cross-cultural universals in behaviour. Universality in complex adaptive human behaviour is often taken as a hallmark of highly specialized innate predispositions (e.g. Buss 1989; Pinker & Bloom 1990). However, since cumulative cultural evolution can similarly result in complex adaptive behaviour, the issue is really whether it also results in convergence in behaviour, such that separate populations independently invent and retain similar behaviours. While culture is generally viewed as a source of behavioural variation between cultures, under certain circumstances it may result in cross-cultural convergence. We explain in §5 how our experimental work has so far contributed to this question.

Clearly, therefore, there are currently some extremely interesting intellectual disputes within the field of cumulative cultural evolution, each of which could benefit from empirical studies of this phenomenon. In §2 we will examine existing approaches to studying cumulative cultural evolution, and what these studies have so far been able to contribute.

2. APPROACHES TO STUDYING CUMULATIVE CULTURAL EVOLUTION

(a) *Studying cumulative cultural evolution in the field*

In order to study the phenomenon of cumulative cultural evolution in natural populations, it is necessary to have access to fairly accurate information about the

past forms of behaviours. This can be difficult because many behaviours leave no discernable trace. However, it is possible to study cumulative cultural evolution from cultural artefacts, including archaeological findings. For example, we can infer from the archaeological record (or rather, the lack of it) that any tools used by hominids up until *ca* 2 million years ago were probably comparable with those used by other great apes, such as chimpanzees (Ambrose 2001). We also know that, approximately a quarter of a million years ago, tools manufactured by humans began to show rapid change and development. Around this time, a wide variety of different stone tools were being used by humans, each tailored to a specific function.

Some authors have documented progress in science and technology in explicitly evolutionary terms (e.g. Wilder's 1968 *Evolution of Mathematical Concepts*; Basalla's 1988 *The Evolution of Technology*). In other texts, the notion of accumulation is more implicit. Inventions and discoveries are dated and advancement is assumed (e.g. Bunch & Hellemans 2004). However, irrespective of the source consulted, evidence can readily be found for ratcheting, with new developments building on previous ones. The loss of information or skills from a population is very much the exception, rather than the rule (although it is worth noting that such loss certainly has been documented; the decline in complexity of the Tasmanian toolkit is probably the best known example, e.g. Henrich 2004).

Consider two examples, the wheel and the mathematical notation. The invention of the wheel as an aid to transportation is generally dated between 5000 and 6000 years ago, with early wheels constituting simple wooden discs with a hole for the axle. The spoked wheel was invented only more recently (*ca* 4000 years ago). The invention of the wheel then gave rise to a number of other technological innovations including cogs and pulleys (Basalla 1988; Bunch & Hellemans 2004). Mathematical systems of notation have also developed considerably over time, with simple tally systems recorded from *ca* 30 000 years ago. However, more abstract symbolic representations are much more recent. Place-value notation was being used by the Mesopotamians by *ca* 4000 years ago, but also seems to have been independently invented by the Indians within the last 2000 years, leading to our current 'Arabic' notation. The invention of a symbol to represent zero (which made the place notation system considerably more informative) was more recent still, in both cultures (Wilder 1968; Bunch & Hellemans 2004).

Clearly, valuable information can be gleaned from studying cumulative cultural evolution in natural populations. Important insights can be gained into the kinds of behaviours that show cumulative cultural evolution over time and the nature of the changes that occur. These can, up to a point, address certain issues raised in §1. For example, adequate information on the past forms of behaviour in populations that have had little contact with one another could enhance our understanding of convergence in cumulative cultural evolution, and therefore the extent to which it may explain cross-cultural universals. However, there are limitations to the kinds of questions one can ask when using these kinds of data. Mesoudi (Mesoudi 2007;

Mesoudi & O'Brien 2008) has argued that historical methods have several drawbacks when it comes to studying cultural variation, and the same apply for investigations of cumulative cultural evolution. The main weakness of this approach, certainly from the perspective of addressing some of the debates listed above, is that it does not allow for the manipulation of variables of interest. We can ask questions about how cumulative cultural evolution *has* occurred, but we cannot ask what *might* have happened, had circumstances been slightly different. By contrast, using an experimental approach, we can explicitly manipulate factors believed to be crucial in generating cumulative cultural evolution, to test hypotheses about necessary precursors. Likewise we can set out to study the outcomes of cumulative cultural evolution in multiple replicated populations under controlled conditions.

(b) *Theoretical studies of cumulative cultural evolution*

By contrast, theoretical studies of cumulative cultural evolution permit researchers to manipulate as many variables as they desire, and controlling extraneous factors is of course not an issue. There are many theoretical models involving social learning, but only a few have tested hypotheses relevant to the debates detailed previously. For instance, Boyd & Richerson's (1996) paper included a theoretical analysis of why cumulative cultural evolution seems to be a rare phenomenon within the animal kingdom. Their models showed that an ability to copy the behaviour of others becomes more useful than a capacity for individual learning only when other members of the population are themselves engaging in behaviours with higher pay-offs than would be achieved by individual learning alone. Hence there is a significant obstacle to the evolution of such capabilities since they are valuable only once they are widespread in the population. Enquist & Ghirlanda (2007) have addressed the issue of the cognitive abilities necessary for cumulative cultural evolution. As mentioned above, their models indicate that a mechanism that can selectively filter out maladaptive behaviours would be crucial for cumulative cultural evolution to evolve. Work by Kirby and colleagues (e.g. Kirby & Christiansen 2003; Smith *et al.* 2003; Kirby *et al.* 2007; Smith & Kirby 2008) has investigated the question of whether complex innate competencies are a necessary feature for the evolution of structured language. Modelling iterated learning of communication systems, they have shown that structural features, such as compositionality, can arise through cultural transmission over multiple generations.

However, the great strength of theoretical models, in terms of the flexibility afforded, is also to an extent their weakness. The constraints imposed on the models are those selected by their creator, and the conclusions drawn necessarily depend on the underlying assumptions, which may or may not be accurate. By contrast, in experimental studies with human subjects, one can gain important insights into the likely results of real learning processes repeated over multiple generations. In §3–6 we detail experimental approaches that can be used to study culture in the laboratory (§3), and explain

how we have applied these methods to test hypotheses about cumulative cultural evolution (§4).

3. STUDYING CULTURE IN THE LABORATORY

There are a variety of methods that have been used for studying culture under laboratory conditions (for reviews see: Mesoudi 2007; Mesoudi & Whiten 2008; Whiten & Mesoudi 2008). The aim of such approaches is essentially to simulate cultural phenomena on a small scale, allowing researchers to study how behaviours change over time as a result of repeated learning and transmission between individuals. While experimental approaches inevitably have imperfections of their own, we consider that the power to manipulate variables and collect precisely the data that are required, constrained and informed by the behaviour of real participants strikes a very constructive balance.

The use of such methods is best illustrated with an example of this kind of study. Jacobs & Campbell (1961) used laboratory 'microcultures' (Gerard *et al.* 1956) aiming to 'demonstrate a perpetuation of 'cultural' characteristics that transcends the replacement of individual persons' (p. 649). Their study therefore involved simulating generational succession through the repeated removal and replacement of participants within small groups. Jacobs & Campbell (1961) wanted to determine whether participants' tendencies to conform to majority opinion could result in long-lasting traditions of counter-intuitive beliefs. Groups were founded by experimental confederates, instructed to respond with a significant overestimation of their true perception of the strength of a visual movement illusion, but these were gradually replaced by naive participants. In an example of one of Jacobs & Campbell's (1961) conditions, there were three individuals present in the test group at any one time, and at the start of the experiment two of these individuals were confederates and one was a naive participant. Each individual from the group was asked to estimate the degree of the illusory movement perceived, starting with the confederates, and their responses were recorded. This was repeated 30 times, after which one of the confederates was removed and replaced by another naive participant. Then 30 more trials were carried out with this new group, and the remaining confederate was then removed and replaced with a further naive participant. This procedure continued for a total of 10 'generations'. Jacobs & Campbell (1961) also ran further conditions, manipulating the size of the test group (varying between one individual and four) and the number of confederates in the first generation (varying between zero and three). Each experimental condition was replicated three times each. Jacobs & Campbell (1961) found that the overestimation bias induced by the confederates persisted for several generations after the final confederate had been removed.

Similar methods, involving the removal and replacement of participants within groups, have since been adopted by Insko *et al.* (1980, 1983) and also more recently by Baum *et al.* (2004). The benefit of this method lies not only in the power to manipulate certain key variables (e.g. the size of group and the number of confederates for Jacobs & Campbell 1961), but also in

the time scale required for the study. While cultural evolution is generally assumed to occur on a time scale of multiple human lifespans, these experiments seek to study cultural phenomena over learner generations, rather than reproductive generations. For this reason, such methods have also been applied within the literature on animal social learning (e.g. Galef & Allen 1995; Laland & Williams 1997, 1998).

As well as methods involving removal and replacement of participants in groups, there are also other methods that can be used to study culture under experimental conditions (for a comprehensive reviews see Mesoudi 2007; Mesoudi & Whiten 2008; Whiten & Mesoudi 2008), but these are less relevant in terms of finding an experimental model for studying cumulative cultural evolution. For example Bartlett (1932) made use of the 'method of serial reproduction' in his studies of human memory, a method that has been recently revived by Mesoudi and colleagues (Mesoudi & Whiten 2004; Mesoudi *et al.* 2006). Although chains of multiple generations are involved, with new participants learning from previous learners, it is quite different from the method detailed above in a number of important respects. In this type of research, participants are explicitly instructed to copy, in that their aim is to reproduce information as accurately as they possibly can. The focus is therefore on the degradation of the information originally provided to the first participant. While this is an excellent method for revealing people's unconscious cognitive biases (as it allows researchers to investigate what sort of information is omitted, or introduced, when participants are actively trying to reproduce material as accurately as possible), it is clearly considerably less appropriate for studying cumulative cultural evolution. Any laboratory model of cumulative cultural evolution must involve behaviours that can show measurable improvement over generations, and it is also important that participants understand that the choice of whether or not to copy is their own.

Until recently, even the experimental work that has been carried out using the replacement method has fallen short of providing an adequate model of cumulative cultural evolution. As noted above, the behaviours to be transmitted must be capable of showing measurable improvement over generations, as a consequence of accumulated modifications. The perceptual judgement task used by Jacobs & Campbell (1961) is therefore far too simple a behaviour. Work carried out by Baum *et al.* (2004; as well as other work from the same group, e.g. McElreath *et al.* 2005, 2008; Efferson *et al.* 2007, 2008) does show increasingly adaptive choices made by participants over generations, but these experiments involve participants choosing between two options each of which has an unpredictable pay-off. This method has been used to elucidate participants' strategies in gauging their use of socially and individually acquired information in order to make best guess choices. In terms of studying cumulative cultural evolution, however, the method is less appropriate. While the average pay-offs seem to increase over time, as a result of participants gravitating towards the choice that is the best on average, the behaviours themselves (of one choice over another) are

not ideal candidates in terms of demonstrating the accumulation of modifications.

Interestingly, in Insko's studies (Insko *et al.* 1980, 1983), which involved between-group trading of paper origami products manufactured by group members, groups made increasingly greater profits over generations, suggesting more efficient methods of production were being passed on. However, it is unclear what the nature of the improved efficiency was and whether this was definitely attributable to transmission between generations. In §4 we detail the method that we have developed for studying cumulative cultural evolution experimentally. Within this issue, studies reported by Fay *et al.* (2008) and Flynn (2008) show similar effects to ours, which may also provide promising approaches for studying cumulative cultural evolution.

4. A METHOD FOR STUDYING CUMULATIVE CULTURAL EVOLUTION IN THE LABORATORY

(a) *The tasks*

As explained above, the task presented to participants must be chosen very carefully in order to create an effective laboratory model of cumulative cultural evolution. It was important that we chose a task that could show measurable improvements in performance over generations, based on the accumulation of modifications. A task with a clear aim and an objective measure of success was therefore crucial, as we needed to be able to show that participants' scores were, on average, better the further they were down the chain (therefore showing that the skills and knowledge had accumulated over the learner generations). It was also important for our design to choose tasks that were simple and easy enough for participants to complete in a short space of time, in order to make these feasible laboratory methods. However, the tasks also needed to be sufficiently difficult and complex that definite benefits could be obtained from opportunities for social learning, and that the accumulation of modifications could be documented.

We have so far used two different tasks in our laboratory studies of cumulative cultural evolution (Caldwell & Millen 2008). In one of our tasks, participants are asked to build a paper aeroplane, the goal being to build one that will fly as far as possible. In the other task, participants are asked to build a tower out of spaghetti and modelling clay. The goal for this task is to build a tower that is as high as possible. Hence we have our objective measures of the success of each participant in relation to the goals they have been given. Furthermore, the tasks that we have selected show similarities with certain examples of early human material culture, such as projectile point shaping and shelter construction. From our point of view, this is also helpful given the types of questions we would like to address with these methods (see §1 above). The tasks therefore have much in common, but there are also important differences between them. First, while many people have some prior experience of having built a paper aeroplane, the spaghetti tower task is far more novel and participants have few preconceived ideas about how to approach the task. Second, while feedback on performance on the spaghetti tower task is continual

time minutes	participants present in test group									
00.00	1	2	3							
02.30	1	2	3	4						
05.00		2	3	4	5					
07.30			3	4	5	6				
10.00				4	5	6	7			
12.30					5	6	7	8		
15.00						6	7	8	9	
17.30							7	8	9	10
20.00								8	9	10
22.30									9	10
25.00										10

Figure 1. Group composition over time in the microsocety design. Generational succession is simulated through the repeated removal of experienced participants and introduction of naive participants. Each row of the table shows the group composition at any given time, made up of observing participants (grey) and participants actually engaged in the task (black). Participants were randomly assigned the positions 1–10.

during construction (participants can of course see exactly how high their tower currently is), feedback on performance on the paper aeroplane task is delayed until construction is complete.

(b) The design

We used a replacement method, with each chain totalling 10 individuals. For each task, we ran 10 replicates of these chains of 10 participants. Figure 1 shows a schematic of the replacement design, indicating which participants were present in the test group at what point during each trial. Participants were randomly assigned to the positions 1–10 in each chain. In order to simulate generational succession, the participants' start times were staggered, such that every 2.5 min a new person entered the group. While they were in the test group, each participant had 5 min of observation time, during which they could watch the previous participants building their artefact, followed by 5 min of building time, during which they had to construct their own artefact. Once their time was up, they left the test group. The staggered start and finish times had the effect that, at any given time (except at the very start and very end of any given chain), there were four individuals together in the group, two of whom were observing and two of whom were actually engaged in the task (figure 1). So, for example, a chain would begin with participant 1 building their artefact, with participants 2 and 3 observing. Then, after 2.5 min, participant 2 would also start building and participant 4 would join the group as an observer. The aim was to simulate a miniaturized society, in which one generation would have the opportunity to interact with and observe individuals from the previous two generations, but not those further back. However, we did retain all artefacts for inspection by later participants, to reflect the more permanent record generated by material culture. The experimenter wrote down the relevant measurements next to each, so that this information was also available. Participants left the testing area once their artefact had been evaluated.

(c) The ratchet effect

Our results showed clear evidence for improvement in performance over the course of the chains (Caldwell & Millen 2008). Figure 2 shows these results for both the paper aeroplanes and the spaghetti towers. Figure 2a(i),b(i) shows the results for each of the 10 chains separately, so each differently coloured line represents a different chain. As is clear from these figures, performance overall can be extremely variable. However, when we (Caldwell & Millen 2008) analysed the trends over generations, a strong effect of improvement in terms of the goal measures (of plane flight distance and tower height) was found. Figure 2a(ii), b(ii) shows the average score for the participants in each position in the chain and illustrates the steady improvement much more clearly. Thus, skills and knowledge do indeed appear to accumulate in the chains, independent of individual membership, consistent with the predictions assuming cumulative cultural evolution. Furthermore, similar patterns were found for both the tasks, in spite of the differences between them, suggesting that we are tapping into a fairly general phenomenon.

(d) Accumulation of modifications

As well as looking for improvement in performance over generations, we were also interested in investigating the inheritance of modifications. We predicted that designs would be more similar within chains than they were across chains (indicating cultural variation), and also that designs that were close together in the chain would be more similar to one another than those that were far apart (indicating descent with modification). For this reason, we took photographs of all the artefacts that had been created by participants, and we were able to use these to test predictions regarding the similarity of designs. The photographs were rated by naive coders, each of whom was given one of the photographs from the set and asked to rate it in comparison with all the others. The coders were provided with a seven-point scale, which they were to refer to in making their ratings. For full details of the methods used to obtain and analyse these ratings, see Caldwell & Millen (2008). As predicted, artefacts from the same chain were rated as more similar than those from different chains, for both the paper aeroplanes and the spaghetti towers. Designs from positions close together in the chains were also more similar than those from positions far apart in chains, demonstrating that the improvement in performance was associated with the accumulation of modifications.

5. APPLICATIONS OF THESE METHODS

We see great potential for using these methods in order to test hypotheses about cumulative cultural evolution. In this section we discuss how some of our work to date has helped to address some of the issues raised in the introduction. We start by discussing our findings regarding cultural convergence, and explain the implications for the potential role of cumulative cultural evolution in human behavioural universals. We also discuss experiments explicitly designed to test hypotheses about learning mechanisms involved in

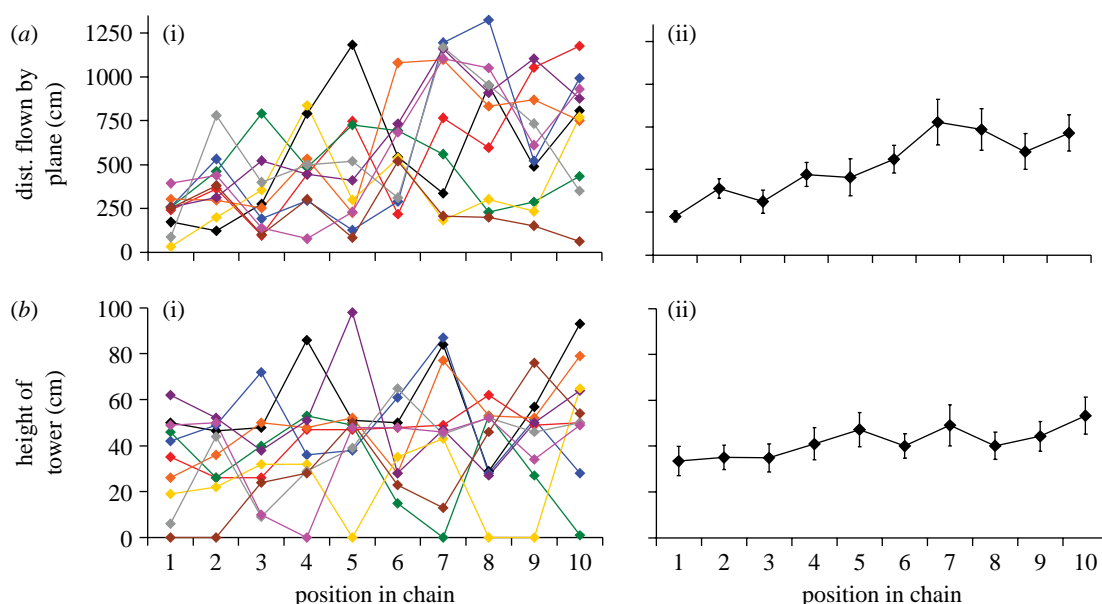


Figure 2. Measures of success over generations. (a(i)) The data for the 10 chains of paper aeroplanes, with (a(ii)) showing the mean distance flown for each position in the chains (error bars indicate \pm s.e.m.). (b(i)) The data for the 10 chains of spaghetti towers, with (b(ii)) showing the mean height for each position in the chains (error bars indicate \pm s.e.m.). Redrawn from Caldwell & Millen (2008).

cumulative cultural evolution. This work has obvious implications for the debate surrounding the cognitive precursors of cumulative cultural evolution, but is also relevant to the debate regarding the uniqueness (or otherwise) of this phenomenon to humans.

(a) *Convergence in cumulative cultural evolution*

As mentioned in §1, questions about the possible role of cumulative cultural evolution in complex human behavioural universals essentially centre on the issue of whether separate cultures are likely to independently invent and retain similar behaviours. We have already been able to investigate this issue, based on the same dataset already discussed (Caldwell & Millen 2008).

In biological evolution, convergent evolution refers to a process by which species that are only distantly related independently evolve analogous adaptations in response to similar environmental pressures. Convergent cultural evolution therefore refers to situations in which different populations independently develop similar socially transmitted behaviours despite different ancestral histories (Caldwell *in press*). In evolutionary biology, distinctions are therefore also drawn between traits that are homologous and analogous. Homology refers to the 'relationship of two characters that have descended, usually with divergence, from a common ancestral character' (Fitch 2000, p. 227). By contrast, analogy 'is distinguished from homology in that its characters, although similar, have descended convergently from unrelated ancestral characters.' (Fitch 2000, p. 227).

Likewise, it is an important question when studying cross-cultural similarities, whether those similarities are the result of common cultural descent or convergence from contrasting ancestral forms. In our experiments it is possible to study the extent to which convergence occurs, since we can control the contact that different microcultures have with one another.

As noted in §4*d*, we had all our photographs of participants' planes and towers rated for their similarity to one another. As well as using these ratings to look into the accumulation of modifications, we were also able to use the ratings to test for convergent cultural evolution (i.e. increasing similarity between the different chains, over generations). This would be predicted because successful designs are liable to have features in common, so the later designs ought to be rated as more similar to one another, compared with earlier designs, due to the fact that they have in effect been shaped by similar selection pressures. In order to analyse this, we took the similarity ratings for all pairs of photographs that were in the same position across chains. Positive correlations were found between the position in the chain and the mean similarity ratings, for both tasks. These results are displayed in figure 3.

We are by no means the first to show that 'iterated learning', i.e. each generation learning from data generated by the previous one, can result in convergence across different microsocieties. Kalish *et al.* (2007), for example, have well illustrated that learners' biases interfere with transmitted information in consistent ways, resulting in different chains of learners—who have often been provided with quite different information to start with—passing on very similar data (see also Griffiths *et al.* 2008). However, such findings, albeit fascinating, may not contribute greatly to the question of whether cumulative cultural evolution could present an alternative account of the existence of complex human behaviours. As noted in §1, Tomasello (1999) has argued that cumulative cultural evolution could explain why human behaviour is so different from that of the other great apes. In effect, the suggestion is that these behaviours are the result of the accrued learning of many generations, rather than the result of natural selection. The finding that cultural transmission degrades information in the

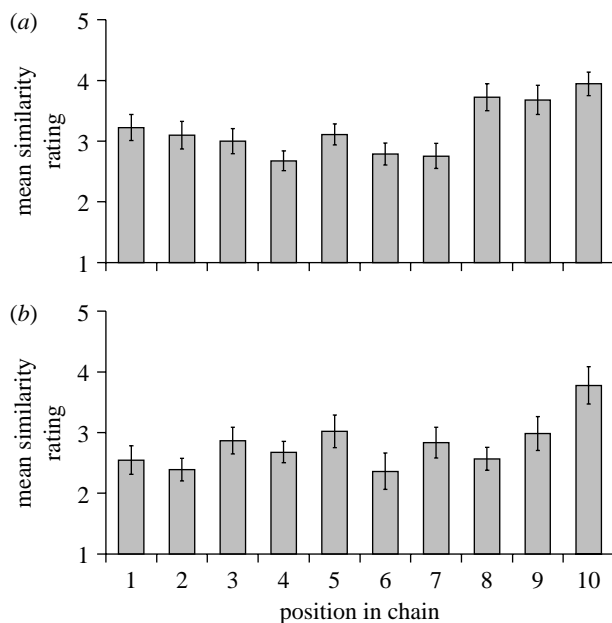


Figure 3. Ratings of similarity for pairs of artefacts in the same position across chains. The data for (a) paper aeroplanes and (b) spaghetti towers. Error bars indicate \pm s.e.m. Redrawn from Caldwell & Millen (2008).

general direction of learners' innate biases therefore does not add much to this particular issue.

By contrast, our results show that increasing cultural similarity can go hand in hand with increasing adaptive complexity. Although universality in complex human behaviour is often attributed to specialized innate predispositions, our results imply that similar behaviours may well be independently discovered and passed on within different populations. It is in fact examples such as ours, which show cumulative cultural evolution being shaped by feedback from multiple attempts, which serve to emphasize just what is so useful about cumulative cultural evolution (e.g. Henrich & McElreath 2003). It is a means by which information is gained, and then retained, within populations. The extended learning period afforded allows us to make discoveries that would not have been possible within a single lifetime. While our experiments are so simple, small scale and short term, as to somewhat trivialize this point, our findings are nonetheless illustrative of phenomena that we believe to be operating over much longer time scales, in many realms of behaviour.

(b) Learning mechanisms

In our ongoing work, we are using the methods that we have developed to test hypotheses about the learning mechanisms that may be involved in cumulative cultural evolution. It has been proposed that cumulative cultural evolution may depend on a capacity for imitation, and that this may be the reason for its apparent rarity in non-humans. Consequently, we have run experiments (C. A. Caldwell & A. E. Millen 2008, unpublished data) designed to test whether restricting opportunities for imitation, and indeed other forms of social learning, influences the trends that we find towards improvement over generations of learners.

Using our paper aeroplane task detailed previously, we have run a variety of different experimental conditions, in which certain sources of social information are either available or unavailable. While in our previous experiment (Caldwell & Millen 2008) participants could observe the two previous participants in the chain, and discuss the task with them, as well as see the results of their efforts in the form of the completed plane and information about its flight distance, in this study we separated these sources of information. In a series of different experimental conditions, participants had access to information in the form of either: actions only; results only; teaching only; actions plus results; actions plus teaching; results plus teaching; or actions, results and teaching. If imitation (in terms of 'learning to do an act by seeing it done', e.g. Whiten & Ham 1992) is indeed crucial to cumulative cultural evolution, then conditions in which this not possible (i.e. those with no information from actions) ought to show much weaker trends towards improvement over generations.

6. CONCLUSION

In summing up, we believe that the experimental methods that we have developed will prove to be extremely useful tools in helping to understand the phenomenon of cumulative cultural evolution, and that it will be possible to make important contributions to some of the debates that surround this field. We hope that our current findings help to illustrate how scaled-down laboratory tests can be used to investigate fundamental cultural processes.

Ethical approval for this research was granted by the University of Stirling Department of Psychology Ethics Committee.

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ENDNOTE

¹It should be noted that there are many different definitions of culture in the literature. Kroeber & Kluckhohn (1952) identified multiple different definitions from authors from a variety of disciplines. Boyd & Richerson (1985) pointed out that, within Kroeber & Kluckhohn's definitions, there is broad agreement on the notion of culture as socially transmitted heritage peculiar to a particular society, which is why we selected this description. Our criteria for culture in the general sense are therefore intentionally broad and inclusive.

REFERENCES

- Ambrose, S. 2001 Paleolithic technology and human evolution. *Science* **291**, 1748–1753. (doi:10.1126/science.1059487)
- Barbrook, A. C., Howe, C. J., Blake, N. & Robinson, P. 1998 The phylogeny of *The Canterbury Tales*. *Nature* **394**, 839. (doi:10.1038/29667)
- Bartlett, F. C. 1932 *Remembering*. Cambridge, UK: Cambridge University Press.
- Basalla, G. 1988 *The evolution of technology*. Cambridge, UK: Cambridge University Press.
- Baum, W. M., Richerson, P. J., Efferson, C. M. & Paciotti, B. M. 2004 Cultural evolution in laboratory micro-societies including traditions of rule giving and rule following. *Evol. Hum. Behav.* **25**, 305–326. (doi:10.1016/j.evolhumbehav.2004.05.003)

- Boesch, C. 2003 Is culture a golden barrier between human and chimpanzee? *Evol. Anthropol.* **12**, 82–91. (doi:10.1002/evan.10106)
- Boesch, C. & Tomasello, M. 1998 Chimpanzee and human cultures. *Curr. Anthropol.* **39**, 591–614. (doi:10.1086/204785)
- Boyd, R. & Richerson, P. J. 1985 *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- Boyd, R. & Richerson, P. J. 1994 Why does culture increase human adaptability? *Ethol. Sociobiol.* **16**, 125–143. (doi:10.1016/0162-3095(94)00073-G)
- Boyd, R. & Richerson, P. J. 1996 Why culture is common, but cultural evolution is rare. *Proc. Br. Acad.* **88**, 77–93.
- Bunch, B. & Hellemans, A. 2004 *A history of science and technology*. London, UK: Houghton Mifflin.
- Buss, D. M. 1989 Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behav. Brain Sci.* **12**, 1–49.
- Caldwell, C. A. In press. Convergent cultural evolution may explain linguistic universals (commentary on Christiansen & Chater, Language as shaped by the brain). *Behav. Brain Sci.*
- Caldwell, C. A. & Millen, A. E. 2008 Experimental models for testing hypotheses about cumulative cultural evolution. *Evol. Hum. Behav.* **29**, 165–171. (doi:10.1016/j.evolhumbehav.2007.12.001)
- Christiansen, M. H. & Chater, N. In press. Language as shaped by the brain. *Behav. Brain Sci.*
- 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 transmission on the Bolivian Altiplano. *Evol. Hum. Behav.* **28**, 11–17. (doi:10.1016/j.evolhumbehav.2006.05.005)
- Efferson, C., Lalive, R., Richerson, P. J., McElreath, R. & Lubell, M. 2008 Conformists and mavericks: the empirics of frequency-dependent cultural transmission. *Evol. Hum. Behav.* **29**, 56–64. (doi:10.1016/j.evolhumbehav.2007.08.003)
- Enquist, M. & Ghirlanda, S. 2007 Evolution of social learning does not explain the origin of human cumulative culture. *J. Theor. Biol.* **246**, 129–135. (doi:10.1016/j.jtbi.2006.12.022)
- Fay, N., Garrod, S. & Roberts, L. 2008 The fitness and functionality of culturally evolved communication systems. *Phil. Trans. R. Soc. B* **363**, 3553–3561. (doi:10.1098/rstb.2008.0130)
- Fitch, W. M. 2000 Homology: a personal review of some of the problems. *Trends Genet.* **16**, 227–231. (doi:10.1016/S0168-9525(00)02005-9)
- Flynn, E. 2008 Investigating children as cultural magnets: do young children transmit redundant information along diffusion chains? *Phil. Trans. R. Soc. B* **363**, 3541–3551. (doi:10.1098/rstb.2008.0136)
- Galef Jr, B. G. 1992 The question of animal culture. *Hum. Nat.* **3**, 157–178. (doi:10.1007/BF02692251)
- Galef Jr, B. G. & Allen, C. 1995 A new model system for studying behavioural traditions in animals. *Anim. Behav.* **50**, 705–717. (doi:10.1016/0003-3472(95)80131-6)
- Galef Jr, B. G., Manzig, L. A. & Field, R. M. 1986 Imitation learning in budgerigars: Dawson and Foss 1965 revisited. *Behav. Process.* **13**, 191–202. (doi:10.1016/0376-6357(86)90025-2)
- Gerard, R. W., Kluckhohn, C. & Rapoport, A. 1956 Biological and cultural evolution: some analogies and explorations. *Behav. Sci.* **1**, 6–34.
- Gray, R. D. & Jordan, F. M. 2000 Language trees support the express-train sequence of Austronesian expansion. *Nature* **405**, 1052–1055. (doi:10.1038/35016575)
- Griffiths, T. L., Kalish, M. L. & Lewandowsky, S. 2008 Theoretical and empirical evidence for the impact of inductive biases on cultural evolution. *Phil. Trans. R. Soc. B* **363**, 3503–3514. (doi:10.1098/rstb.2008.0146)
- Henrich, J. 2004 Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: the Tasmanian case. *Am. Antiquity* **69**, 197–214. (doi:10.2307/4128416)
- Henrich, J. & McElreath, R. 2003 The evolution of cultural evolution. *Evol. Anthropol.* **12**, 123–135. (doi:10.1002/evan.10110)
- Hermann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B. & Tomasello, M. 2007 Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* **317**, 1360–1366. (doi:10.1126/science.1146282)
- Heyes, C. M. 1993 Imitation, culture and cognition. *Anim. Behav.* **46**, 999–1010. (doi:10.1006/anbe.1993.1281)
- Humle, T. & Matsuzawa, T. 2002 Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *Am. J. Primatol.* **58**, 133–148. (doi:10.1002/ajp.10055)
- Hunt, G. R. & Gray, R. D. 2003 Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc. R. Soc. B* **270**, 867–874. (doi:10.1098/rspb.2002.2302)
- Insko, C. A. *et al.* 1980 Social evolution and the emergence of leadership. *J. Pers. Soc. Psychol.* **39**, 431–448. (doi:10.1037/0022-3514.39.3.431)
- Insko, C. A., Gilmore, R., Drenan, S., Lipsitz, A., Moehle, D. & Thibaut, J. 1983 Trade versus exploration in open groups: a comparison of two types of social power. *J. Pers. Soc. Psychol.* **44**, 977–999. (doi:10.1037/0022-3514.44.5.977)
- Jacobs, R. C. & Campbell, D. T. 1961 The perpetuation of an arbitrary tradition through several generations of laboratory microculture. *J. Abnorm. Soc. Psych.* **62**, 649–658. (doi:10.1037/h0044182)
- Kalish, M. L., Griffiths, T. L. & Lewandowsky, S. 2007 Iterated learning: intergenerational knowledge transmission reveals inductive biases. *Psych. Bull. Rev.* **14**, 288–294.
- Kawai, M. 1965 Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates* **6**, 1–30. (doi:10.1007/BF01794457)
- Kawamura, S. 1959 The process of sub-culture propagation among Japanese macaques. *Primates* **2**, 43–60. (doi:10.1007/BF01666110)
- Kenward, B., Weir, A. A. S., Rutz, C. & Kacelnick, A. 2005 Tool manufacture by naive juvenile crows. *Nature* **433**, 121. (doi:10.1038/433121a)
- Kirby, S. & Christiansen, M. H. 2003 From language learning to language evolution. In *Language evolution* (eds M. Christiansen & S. Kirby), pp. 272–294. Oxford, UK: Oxford University Press.
- Kirby, S., Dowman, M. & Griffiths, T. L. 2007 Innateness and culture in the evolution of language. *Proc. Natl Acad. Sci. USA* **104**, 5241–5245. (doi:10.1073/pnas.0608222104)
- Kroeber, A. L. & Kluckhohn, C. 1952 Culture, a critical review of the concepts and definitions. *Pap. Peabody Museum Am. Archeol. Ethnol.* **47**, 1–233.
- Laland, K. N. 2004 Social learning strategies. *Learn. Behav.* **32**, 4–14.
- Laland, K. N. & Hoppitt, W. 2003 Do animals have culture? *Evol. Anthropol.* **12**, 150–159. (doi:10.1002/evan.10111)
- Laland, K. N. & Williams, K. 1997 Shoaling generates social learning of foraging information in guppies. *Anim. Behav.* **53**, 1161–1169. (doi:10.1006/anbe.1996.0318)
- Laland, K. N. & Williams, K. 1998 Social transmission of maladaptive information in the guppy. *Behav. Ecol.* **9**, 493–499. (doi:10.1093/beheco/9.5.493)

- McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., Efferson, C. & Paciotti, B. 2005 Applying evolutionary models to the laboratory study of social learning. *Evol. Hum. Behav.* **26**, 483–508. (doi:10.1016/j.evolhumbehav.2005.04.003)
- McElreath, R., Bell, A. V., Efferson, C., Lubell, M., Richerson, P. J. & Waring, T. 2008 Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. *Phil. Trans. R. Soc. B* **363**, 3515–3528. (doi:10.1098/rstb.2008.0131)
- Mesoudi, A. 2007 Using the methods of experimental social psychology to study cultural evolution. *J. Soc. Evol. Cultur. Psychol.* **1**, 35–58.
- Mesoudi, A. & O'Brien, M. J. 2008 The cultural transmission of Great Basin projectile-point technology I: an experimental simulation. *Am. Antiquity* **73**, 3–28.
- Mesoudi, A. & Whiten, A. 2004 The hierarchical transformation of event knowledge in human cultural transmission. *J. Cogn. Cult.* **4**, 1–24. (doi:10.1163/156853704323074732)
- Mesoudi, A. & Whiten, A. 2008 The multiple roles of cultural transmission experiments in understanding human cultural evolution. *Phil. Trans. R. Soc. B* **363**, 3489–3501. (doi:10.1098/rstb.2008.0129)
- Mesoudi, A., Whiten, A. & Laland, K. N. 2004 Is human cultural evolution Darwinian? Evidence reviewed from the perspective of *The Origin of Species*. *Evolution* **58**, 1–11. (doi:10.1554/03-212)
- Mesoudi, A., Whiten, A. & Dunbar, R. 2006 A bias for social information in human cultural transmission. *Br. J. Psychol.* **97**, 405–423. (doi:10.1348/000712605X85871)
- Pinker, S. & Bloom, P. 1990 Natural language and natural selection. *Behav. Brain Sci.* **13**, 707–727.
- Richerson, P. J. & Boyd, R. 2005 *Not by genes alone: how culture transformed human evolution*. Chicago, IL: University of Chicago Press.
- Smith, K. & Kirby, S. 2008 Cultural evolution: implications for understanding the human language faculty and its evolution. *Phil. Trans. R. Soc. B* **363**, 3591–3603. (doi:10.1098/rstb.2008.0145)
- Smith, K., Brighton, H. & Kirby, S. 2003 Complex systems in language evolution: the cultural emergence of compositional structure. *Adv. Complex Syst.* **6**, 537–558. (doi:10.1142/S0219525903001055)
- Sugiyama, Y. 1997 Social tradition and the use of tool-composites by wild chimpanzees. *Evol. Anthropol.* **6**, 23–27. (doi:10.1002/(SICI)1520-6505(1997)6:1<23::AID-EVAN7>3.0.CO;2-X)
- Tehrani, J. & Collard, M. 2002 Investigating cultural evolution through biological phylogenetic analyses of Turkmen textiles. *J. Anthropol. Archaeol.* **21**, 443–463. (doi:10.1016/S0278-4165(02)00002-8)
- Tomasello, M. 1990 Cultural transmission in tool use and communicatory signalling of chimpanzees. In *“Language” and intelligence in monkeys and apes: comparative developmental perspectives* (eds S. Parker & K. Gibson), pp. 274–311. Cambridge, UK: Cambridge University Press.
- Tomasello, M. 1999 *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tomasello, M., Kruger, A. C. & Ratner, H. H. 1993 Cultural learning. *Behav. Brain Sci.* **16**, 495–552.
- Whiten, A. & Ham, R. 1992 On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Adv. Stud. Behav.* **21**, 239–283. (doi:10.1016/S0065-3454(08)60146-1)
- Whiten, A. & Mesoudi, A. 2008 Establishing an experimental science of culture: animal social diffusion experiments. *Phil. Trans. R. Soc. B* **363**, 3477–3488. (doi:10.1098/rstb.2008.0134)
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C., Wrangham, R. & Boesch, C. 1999 Cultures in chimpanzees. *Nature* **399**, 682–685. (doi:10.1038/21415)
- Whiten, A., Horner, V. & Marshall-Pescini, S. 2003 Cultural panthropology. *Evol. Anthropol.* **12**, 92–105. (doi:10.1002/evan.10107)
- Wilder, R. L. 1968 *Evolution of mathematical concepts: an elementary study*. London, UK: Wiley.