

## Durham Research Online

---

### Deposited in DRO:

04 August 2014

### Version of attached file:

Accepted Version

### Peer-review status of attached file:

Peer-reviewed

### Citation for published item:

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

### Further information on publisher's website:

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

### Publisher's copyright statement:

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

## Use policy

---

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

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

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

Please consult the [full DRO policy](#) for further details.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25

**HUMAN CUMULATIVE CULTURE: A COMPARATIVE PERSPECTIVE**

Lewis G. Dean<sup>1§\*</sup>, Gill L. Vale<sup>2§\*</sup>, Kevin N. Laland<sup>1</sup>, Emma Flynn<sup>3</sup> and Rachel L. Kendal<sup>2\*</sup>

<sup>1</sup>Centre for Social Learning and Cognitive Evolution, School of Biology, University of St. Andrews, St. Andrews, Queen’s Terrace, St. Andrews, Fife. KY16 9TS

<sup>2</sup>Centre for Coevolution of Biology & Culture, Department of Anthropology, Durham University, Dawson Building, Mount Joy Site, Durham. DH1 3LE

<sup>3</sup>Centre for Coevolution of Biology & Culture, Department of Psychology, Durham University, Mount Joy Site, Durham. DH1 3LE

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

§Both authors contributed equally to this paper.

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

28<sup>th</sup> April 2013

26	I.	How is culture cumulative?
27	II.	Culture in animals
28	(1)	Defining culture
29	(2)	The animal culture debate
30	III.	Cumulative culture
31	IV.	Evidence for cumulative culture
32	(1)	Human cumulative culture
33	(a)	Historical evidence
34	(b)	Empirical research
35	(2)	Non-human cumulative culture
36	(a)	Evidence from the wild
37	(b)	Empirical testing of non-human cumulative culture
38	V.	Differences in cumulative culture between humans and non-humans?
39	(1)	Hypotheses concerning the lack of cumulative culture in non-
40		humans
41	(a)	Cognitive differences
42	(i)	Innovation
43	(ii)	Conservatism
44	(iii)	Imitation
45	(iv)	Adaptive filtering
46	(v)	Teaching
47	(vi)	Complex communication
48	(vii)	Prosociality
49	(b)	Social learning strategies
50	(i)	Conformity
51	(ii)	Selective copying
52	(c)	Social structure
53	(i)	Monopolisation
54	(ii)	Scrounging
55	(d)	Demography
56	(2)	Efficiencies and complexities
57	VI.	Conclusions
58		

59 **ABSTRACT**

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

79

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

82 **I. HOW IS CULTURE ‘CUMULATIVE’?**

83

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

94 The focus of this review is cumulative culture, the ability of humans to  
95 ratchet up the complexity of cultural traits over time. The example of the Apollo  
96 mission demonstrates that humans are able to increase the complexity of their  
97 technology and knowledge over many episodes of social transmission, by  
98 building on the developments of their predecessors. This ratcheting up in the  
99 complexity of cultural traits, frequently across multiple generations, has been  
100 proposed to be the hallmark of human culture (Richerson & Boyd, 2005; Enquist  
101 & Ghirlanda; Mesoudi, 2011a), but the cognitive and social processes upon which  
102 it relies remain poorly understood. Here a comparative perspective is potentially  
103 informative. While claims have been made that certain animals possess  
104 cumulative culture in rudimentary form, these are disputed and the human  
105 capacity for cumulative culture is clearly unparalleled in the animal kingdom.  
106 The question of what underlies this difference in human and animal cultures was

107 featured in *Science* magazine's (2005) list of 100 things we don't know that we  
108 need to, as the answer to this question has far reaching implications for how we  
109 view our place in nature.

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

115

## 116 **II. CULTURE IN ANIMALS.**

117

### 118 **(1) Defining culture.**

119 The term 'culture' is used by researchers from a broad range of disciplines,  
120 including biology, psychology, archaeology, social and biological anthropology,  
121 with each discipline drawing on different epistemological and ontological  
122 assumptions. As Sterelny (2009) points out, these different definitions of culture  
123 are not stipulative, they are hypothesis choosing. Thus, through formulating a  
124 definition, researchers have determined their focus, thereby limiting both what  
125 is investigated and how it is investigated. Using different definitions, the focus of  
126 the study of culture can cover over 11,000 species (Lumsden & Wilson, 1981) or  
127 be restricted to humans (Kroeber & Kluckhorn, 1952). The definitions ascribed  
128 to culture can impose constraints on which learning processes are deemed to  
129 underlie culture (e.g. "Culture is information capable of affecting individuals'  
130 phenotypes, which they acquire from other conspecifics by teaching or  
131 imitation", (Boyd & Richerson, 1985, page 33). Moreover, the definition also

132 dictates whether culture is treated as the physical expression of specific  
133 behaviour patterns (van Schaik et al., 2003) or as the ideas and beliefs which lie  
134 behind behaviour patterns (D'Andrade, 2008).

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

141

## 142 **(2) The animal cultures debate.**

143 Alongside the alternative definitions that different researchers apply to culture,  
144 there are also disagreements about the quality of the evidence necessary for a  
145 given species to be deemed ‘cultural’ (Galef, 1992; Laland & Hoppitt, 2003;  
146 Laland & Galef, 2009). For instance, Lefebvre and Palameta (1988) summarise  
147 nearly 100 reports of traditional behavioural patterns in animal species,  
148 including mammals, birds and fish, suggesting that animal traditions are  
149 taxonomically widespread. Although these authors did not classify these  
150 phenomena as ‘culture’, to the extent that the observation of a tradition can be  
151 regarded as evidence for social transmission, these species are potentially  
152 candidates for animal culture. However, it is difficult to establish unequivocally  
153 that social transmission underlies natural diffusions and inter-population  
154 behavioural variation, since individual animals might independently have been  
155 shaped by ecological conditions to perform the focal behaviour. For this reason,  
156 some researchers seek additional evidence that natural traditions are socially

157 transmitted, for instance, relying on translocation experiments or careful  
158 analyses of the development of the behaviour. In reviewing field experiments,  
159 Reader and Biro (2010) concluded that social learning has been unequivocally  
160 demonstrated in 20 different species in the wild, including in honeybees, birds  
161 and mammals, and across a range of contexts, including foraging, predator  
162 avoidance and habitat choice. Whilst these experiments do not necessarily test  
163 whether the behaviour patterns are group typical, they do establish that the  
164 relevant information is socially transmitted. However, given that many hundreds  
165 of species of animals have been shown to be capable of social learning through  
166 experiments in captivity, this list almost certainly substantially underestimates  
167 the extent of natural animal tradition.

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



181           These claims have been criticised by other researchers concerned that the  
182 reports of culture in primates are based upon purely observational studies, with  
183 no experimental evidence that the behavioural variation is indeed a result of  
184 socially transmitted information and not some other factor (Galef, 1992;  
185 Tomasello, 1994; Laland & Hoppitt, 2003). While such experimental procedures  
186 are available (e.g. manipulations in which individuals are experimentally  
187 transferred between populations, or populations are transferred between sites),  
188 and have been applied to some fish species (Helfman & Schultz, 1984; Warner,  
189 1988), they are not feasible for primates. More recently, less disruptive methods  
190 have been developed for identifying social learning in the field (Laland et al.,  
191 2009; Kendal et al., 2010b).

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

196

### 197 **III. CUMULATIVE CULTURE.**

198 The idea of cumulative culture is integral to the work of cultural evolutionists  
199 (Cavalli-Sforza & Feldman, 1981; Lumsden & Wilson, 1981; Boyd & Richerson,  
200 1985), who have developed mathematical models, based on those used in  
201 evolutionary biology, to examine how cultural innovations are introduced and  
202 spread within a population. Whilst this work was primarily focussed on culture  
203 in humans, other researchers have been interested in a comparative approach to  
204 culture. In 1994 comparative psychologist Michael Tomasello first coined a  
205 metaphor commonly used to illustrate cumulative culture, that of the ‘ratchet’

206 (Tomasello, 1994). Tomasello argued that loss of a cultural trait across  
207 generations is prevented by high-fidelity information transmission conferred by  
208 accurate social learning processes, creating the opportunity for modifications of  
209 the cultural trait to be devised, ratcheting up its complexity or efficiency. Over  
210 time, repeated modifications result in cultural traits that are too complex to have  
211 been invented by a single individual (Tomasello et al., 1993; Tomasello, 1994;  
212 Tomasello, 1999). Several researchers have argued that this cultural ‘ratchet’ is a  
213 unique feature of human culture (Heyes, 1993; Tomasello et al., 1993; Tomasello,  
214 1994; Boyd & Richerson, 1996). Theoretical analyses provide support for the link  
215 between high-fidelity transmission mechanisms and cumulative culture:  
216 irrespective of the rate of innovation, cumulative culture cannot emerge without  
217 accurate transmission (Lewis & Laland, In Press). Pradham et al (2012) have  
218 suggested that increased sociability, thus an increase in social learning  
219 opportunity, may be sufficient for cumulative culture to occur, although some  
220 researchers argue that high fidelity transmission is not present in non-humans  
221 (Tennie et al., 2009).

222         Some researchers have discussed the accumulation of a large number of  
223 behavioural traits (e.g. knowledge of different foods) as cumulative culture (van  
224 der Post & Hogeweg, 2008). However this accumulation does not necessarily  
225 involve modifications over time, nor any ratcheting up in complexity or  
226 efficiency. Cumulative culture may occur alongside the accumulation of  
227 knowledge or behaviour patterns, but there is a key difference between the two.  
228 Henceforth, we describe as *accumulation*, the addition of knowledge or  
229 behaviour patterns to the behavioural repertoire of an individual or population  
230 (akin to ‘step-wise traditions’, as proposed by Tennie et al. (2009)), and restrict

231 use of the phrase *cumulative culture* to the modification, over multiple  
232 transmission episodes, of cultural traits (behavioural patterns transmitted  
233 through social learning) resulting in an increase in the complexity or efficiency of  
234 those traits.

235

#### 236 **IV. EVIDENCE FOR CUMULATIVE CULTURE.**

237

##### 238 **(1) Human cumulative culture**

###### 239 *(a) Historical evidence*

240 Human culture is clearly cumulative, with innovations being built upon the  
241 knowledge of previous generations and ideas from different disciplines and  
242 populations combined to formulate new traditions and technologies. Lehman  
243 (1947) and Basalla (1988) have both documented the invention, refinement and  
244 propagation of novel innovations across various technological and academic  
245 disciplines (see also: Ziman, 2000). Lehman (1947) found that there had been  
246 rapid advancement in the academic fields of chemistry, genetics, geology,  
247 mathematics, medicine and public hygiene, education, entomology, botany,  
248 philosophy, operatic and symphonic music. Using historical sources  
249 documenting the number of books published or the number of ‘outstanding  
250 contributions’ to a field as judged by several recognised historians, Lehman has  
251 demonstrated exponential growth in these fields on an historical timescale  
252 (starting between 1000–1600 AD through to the 20<sup>th</sup> century). Although  
253 Lehman’s data may be somewhat subjective, he obtained data from multiple  
254 sources on the definition of an ‘outstanding contribution’ in a particular field. He  
255 illustrates that by building upon previous knowledge, humans have accelerated

256 their discovery of knowledge. Indeed he predicted that in the near future this  
257 acceleration would continue and mechanisation would become more important  
258 and widespread, a prediction that, superficially, appears to be true. While  
259 Lehman (1947) does not explicitly examine whether cumulative culture is  
260 occurring, it is reasonable to assume that the contributions reviewed are built on  
261 previous contributions (Enquist et al., 2008).

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

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

275

#### 276 *(b) Human empirical work*

277 Several researchers have investigated cumulative modifications to behavioural  
278 traits using artificial 'generations' in the laboratory. In these diffusion chain  
279 experiments, participants take part in a task in series; thus the first participant  
280 will act as demonstrator to the second participant, who will in turn act as

281 demonstrator to the third participant and so forth (see Mesoudi & Whiten, 2008  
282 for a review).

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

299         Also using a transmission chain design, Flynn (2008) presented children  
300 with puzzle boxes in which a reward was held in place by a series of defences.  
301 Children received an initial demonstration containing both task irrelevant  
302 actions (which had no bearing on gaining the reward) and task relevant actions  
303 (which allowed reward retrieval). The aim was to assess whether children would  
304 copy both the functional and non-functional actions, or whether the irrelevant  
305 actions would be filtered out gradually along the diffusion chain. Flynn found

306 that children did parse out task irrelevant actions, often quite early in the  
307 diffusion chains. Thus the technique that the children employed was gradually  
308 modified across the laboratory 'generations', creating a more efficient means to  
309 gain the reward. Flynn (2008) argues that this modification of the procedure  
310 represents a cumulative improvement in efficiency and, therefore, a cumulative  
311 cultural process.

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

326         A striking finding was that the level of conservatism of design was higher  
327 when pay-offs were less predictable (Caldwell & Millen, 2010a). In this  
328 experiment there were two measuring protocols; in one condition spaghetti  
329 towers were measured immediately upon completion, whilst in a second  
330 condition the towers were measured five minutes after completion and following

331 their transfer to a table upon which was a desk fan. The increase in uncertainty  
332 about whether the tower would remain standing in the breeze from the fan  
333 decreased the amount of modification made to designs over the chain compared  
334 to towers that were measured immediately, raising the possibility that in more  
335 risky situations the ratcheting up of cumulative cultural traits may be hindered.

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

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

353

354 **(2) Non-human cumulative culture.**

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

357

358 *(a) Evidence from the wild*

359 Based on observations of animals in the wild, some researchers have claimed  
360 that other species show cumulative culture. As these observations must allow a  
361 comparison with the cumulative culture that is observed in humans, we suggest  
362 the following criteria be deployed to guide identification of cumulative culture in  
363 other animals. First, there should be evidence that the behavioural pattern or  
364 trait is socially learned and any variation in the character is not solely due to  
365 genetic or environmental factors (Laland & Janik, 2006). Second, there must be  
366 evidence that the character in question changes over time in a directional, or  
367 progressive manner. This requires evidence that it has been transmitted  
368 between individuals through social learning over repeated episodes. It also  
369 requires evidence that the character has changed in the transmission process to  
370 achieve an enhanced level of complexity. For practical reasons, a useful yardstick  
371 is that the character should be beyond what a single individual could have  
372 invented alone (Tennie et al., 2009) (Table 1). The evidence for cumulative  
373 transmission may come from long-term field studies, archaeological finds or  
374 some other source. However, we emphasize that the occurrence of similar, but  
375 non-identical, behaviour patterns in different populations (whether for the same  
376 purpose or different purposes), does not constitute evidence that one evolved  
377 from the other, and that supplementary evidence (e.g. observational,  
378 archaeological) will be required to demonstrate that variation in the character is  
379 attributable to ratcheting, and that cumulative change occurs within a historical



380 lineage. The appearance of similar methods for performing a task in different  
381 populations may reflect the fact that there is a salient, or easily-discoverable,  
382 method of performing that task and not evidence of shared ancestry. Cultural  
383 evolution is likely to occur over a shorter time scale than genetic evolution,  
384 which may also alter behaviour, but over a longer time period.

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

402         The second behaviour pattern outlined as cumulative by Boesch (2003) is  
403 ectoparasite manipulation in the three Eastern chimpanzee communities of  
404 Budongo, Mahale and Gombe. At all three sites leaves are used to inspect the

405 parasites that have been removed during grooming; at Budongo the parasite is  
406 placed on a leaf when removed. However, at Mahale individuals fold the leaf and  
407 then cut it with their nail. At Gombe there is a variant in which several leaves are  
408 piled on top of one another before the parasite is placed on the top and  
409 inspected. However, these are small modifications and there is no direct  
410 evidence that what has been described as the 'modified' behaviour pattern is  
411 derived from the ascribed 'ancestral' behaviour pattern. Whilst the two  
412 hypothetically 'derived' behaviour patterns could each have evolved from the  
413 hypothesised 'ancestral' character, it remains possible that each variant could  
414 have been invented independently.

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

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

430 The complex tool sets observed at some sites, most notably in the central African  
431 communities, appear to be used, in sequence, for different aspects of the same  
432 foraging behaviour (Sanz & Morgan, 2007; Boesch et al., 2009; Sanz & Morgan,  
433 2009; Sanz et al., 2009). One tool is normally used to puncture the outside of a  
434 nest of ants or bees. Other tools are then used to widen the hole to allow greater  
435 access to the food within. Finally, a smaller stick tool is used to gather honey,  
436 ants or larvae. In one study this 'collector' stick was modified to increase the  
437 surface area (Boesch et al., 2009; Sanz et al., 2009), the bark being removed and  
438 the wood below chewed to make it more brush-like. These tool sets contrast with  
439 other populations in which similar behaviour is performed, but with a single tool  
440 (Whiten et al., 1999; Humle & Matsuzawa, 2002). Once again, there is no direct  
441 evidence that any of the single tool or proposed 'simpler' behaviour patterns are  
442 ancestral to the multiple tool or more elaborate variants. Whilst these tool kits  
443 may be a case of simple cumulative culture, without the required evidence it is  
444 currently not clear that they are more complex than a single individual could  
445 invent alone.

446 Perry et al. (2003) reported a number of social conventions that arose in a  
447 population of capuchin monkeys that are also suggestive of cumulative culture.  
448 These social games appear to have derived from the existing hand-sniffing  
449 behaviour (Perry et al., 2003), which has been observed in some populations.  
450 The social games, the hand-in-mouth, hair-in-mouth and toy-in-mouth games  
451 emerged in succession, within one group, with the latter two appearing to be  
452 modifications of the first (Perry et al., 2003). However, whilst this represents an  
453 interesting case of modifications to a social behaviour pattern, all modifications  
454 appear to have been initiated by one individual, Guapo, a young male in the

455 group. Although this demonstrates the ability of individuals in the species to  
456 make small modifications to a behaviour pattern, it does not represent a multi-  
457 generational or even multi-individual behavioural modification. Thus, in the  
458 absence of evidence for repeated bouts of transmission and refinement, this  
459 example too fails to provide clear evidence for cumulative culture, and is better  
460 characterized as several bouts of individual learning building upon one another.

461 More recently, white faced capuchins have been observed performing the  
462 'eye poke' social convention, documented as the poking of a conspecifics finger  
463 into the eye of another (Perry, 2011). 'Eye poking' (to oneself) has interestingly  
464 been reported to occasionally occur concurrent with the 'hand sniff' (Perry,  
465 2008), representing conjunction of the two conventions. Importantly however,  
466 this eye poke convention, along with the other reported social conventions, seem  
467 to have been reinvented in different groups/locations (Perry, 2011), providing  
468 further support that these behaviours are not beyond what individuals can  
469 invent for themselves. Moreover, there is as of yet no evidence that eye-poking  
470 with hand sniff is in any sense superior to the hand sniff alone, which means this  
471 variation may well be better characterised as cultural drift (in which random  
472 changes have occurred, without selection). Hence, these examples, while  
473 representing interesting social traditions, cannot yet be said to be cumulative.  
474 Stone-handling behaviour in Japanese macaques is present in different forms at  
475 sites throughout Japan, although its adaptive significance is unknown (Leca et al.,  
476 2007; Huffman et al., 2008; Nahallage & Huffman, 2008; Leca et al., 2010). Some  
477 variants of the behaviour are almost ubiquitous, while others are rare, leading to  
478 the hypothesis that some individuals may be specialists, who have created new  
479 behavioural variants from existing ones (Leca et al., 2007). However, once again,

480 there is no evidence that even the most complex of the stone-handling  
481 behaviours is outside a single individual's capacity to invent, and the putative  
482 refinements are not unambiguously improvements. If these traits are non-  
483 adaptive, as it is claimed (Leca et al., 2007), then there would seem to be little  
484 reason for there to be conservatism in the behaviour and, therefore, we might  
485 expect to see great diversity in stone-handling modifications in Japanese  
486 macaques through a drift-like process (Caldwell & Millen, 2010a). This would  
487 mean that, rather than any one stone-handling behaviour building in complexity  
488 (or efficiency) upon another, each behaviour may simply represent the  
489 corruption of an existing stone-handling behaviour, inaccurately transmitted  
490 between individuals, without any further addition of complexity. Note that, we  
491 do not dismiss accidental mutations or inaccurate transmission as playing a role  
492 in cumulative culture but, that for ratcheting to occur beneficial 'accidents' would  
493 be preferentially retained.

494       Circumstantial evidence for cumulative modifications can also be found in  
495 New Caledonian crows (Hunt & Gray, 2004; Seed et al., 2007). The species uses  
496 several tools, the most studied of which are constructed from *Pandanus* leaves,  
497 which are used for foraging. Hunt and Gray (2003) document three different  
498 designs of these tools: narrow, wide and stepped. Amongst the stepped designs,  
499 between one and four steps are used. These patterns vary geographically across  
500 New Caledonia. It has been claimed that the variation in *Pandanus* tool design  
501 across New Caledonia is most parsimoniously explained as cumulative variation  
502 (Hunt & Gray, 2003). Hunt and Gray (2003) propose that the wide tools are the  
503 ancestral tools with the narrow and stepped types derived from them. The  
504 variation in stepped tools has also been proposed to be a series of modifications

505 to the original one step design (Hunt & Gray, 2003). However, like chimpanzee's  
506 tools, there is no direct evidence that these lineages are correct and the different  
507 tool types are not individual innovations, each invented from scratch. The  
508 evidence for social learning in the wild is also equivocal, suggesting there is a  
509 significant level of individual invention (Holzhaider et al., 2010) and evidence  
510 from captivity indicates New Caledonian crows may possess an inherited  
511 predisposition for tool use and tool manipulation (Kenward et al., 2005;  
512 Kenward et al., 2006).

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

518

519

Insert Table 1 about here

520

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

522 The first explicit test of the capacity for cumulative cultural learning in non-  
523 human primates found little evidence that chimpanzees could accumulate  
524 modifications to their behaviour (Marshall-Pescini & Whiten, 2008). This test  
525 involved a puzzle box that could be opened in two ways, with the second, more  
526 complicated, method allowing access to nuts and a greater volume of honey than  
527 the first, simpler method, which just allowed animals to dip for honey. The  
528 chimpanzee subjects were allowed to manipulate the puzzle box in a baseline  
529 condition with no demonstration, resulting in two individuals out of 14

530 discovering the first, 'dipping' method, and one also discovering the more  
531 complicated method. When the dipping method was demonstrated by a familiar  
532 human demonstrator three more individuals managed to learn it. These animals  
533 then received a demonstration of the more complicated method; of the five  
534 individuals tested only one performed the more complicated method and this  
535 was the individual who had already discovered the method in the baseline trials.

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

548         Compound tool use, the combining of separate objects to make a meta-  
549 tool, has been observed in wild chimpanzees, on a handful of occasions and only  
550 in certain contexts (Sugiyama, 1997; Boesch, 2003). Price et al. (2009) tested  
551 captive chimpanzees, where subjects were required to put together two  
552 component tools to create an elongated single tool that could be used to retrieve  
553 an out-of-reach food reward. Chimpanzees were significantly more likely to learn  
554 to combine and use the tool when they had seen a video demonstration showing

555 the tool being manufactured and used, than in other conditions, where  
556 individuals received a video demonstration of only part of the process. This  
557 suggests that the participants were able to modify a tool, which they then used to  
558 retrieve food and may have the potential for rudimentary cumulative cultural  
559 learning. However, as some control subjects, who received no demonstration of  
560 the combining process, were also able to learn to make the complex tool, it  
561 clearly is not beyond a single individual's capabilities (Tennie et al., 2009).

562         The most comprehensive experimental attempt to investigate the factors  
563 that may underlie cumulative culture in animals to-date was carried out by Dean  
564 et al (2012). In a comparative study of sequential problem solving, Dean et al  
565 provided groups of capuchin monkeys, chimpanzees, and nursery school  
566 children with an experimental puzzle box that could be solved in three stages to  
567 retrieve rewards of increasing desirability (Figure 1). Stage 1 required  
568 individuals to push a door in the horizontal plane to reveal a chute through  
569 which a low-grade reward was delivered. Stage 2 required individuals to depress  
570 a button and slide the door further to reveal a second chute for a medium grade  
571 reward. Stage 3 required the solver to rotate a dial, releasing the door to slide  
572 still further to reveal a third chute containing a high-grade reward. All stages  
573 could be completed through two parallel options, with sets of three chutes on  
574 both left and right sides. This two-action, two-option design aided evaluation of  
575 alternative social learning mechanisms and allowed two individuals to operate  
576 the puzzle box simultaneously. After 30 hours of presentation of the task to each  
577 of four chimpanzee groups, only 1 of 33 individuals reached stage 3, with a  
578 further 4 having reached stage 2, and with each group having witnessed multiple  
579 solvers at stage 1 (experiment 1). Chimpanzee performance was not greatly



580 enhanced by trained demonstrators (experiment 2). A similar pattern was  
581 observed in the capuchins: after 53 hours, no individual reached stage 3 and only  
582 two individuals reached stage 2. Thus, the experiments provided no evidence for  
583 cumulative learning in chimpanzees or capuchins. These findings stand in stark  
584 contrast to those of the children, where despite a far shorter exposure to the  
585 apparatus (2.5 hours), five out of eight groups had at least two individuals (out of  
586 a maximum of five) who reached stage 3, with multiple solvers at stages 2 or 3 in  
587 all but two groups. Dean et al found that the success of the children, but not of  
588 the chimpanzees or capuchins, in reaching higher-level solutions was strongly  
589 associated with a package of sociocognitive processes—including teaching  
590 through verbal instruction, imitation, and prosociality—that were observed only  
591 in the children. Children’s individual task performance covaried strongly with  
592 the amount of teaching, imitation and other prosocial behaviours (donation of  
593 retrieved stickers) they personally received; those children that received less  
594 support were less likely to get to the higher cumulative stages of the task and all  
595 children who got to the final stage did so with, usually, at least two forms of  
596 social support (Dean et al., 2012). Thus, completion of all stages of the task was  
597 beyond that which an individual child could invent for his/herself. While this  
598 study does not represent a multi-generational approach, it provides evidence for  
599 the socio-cognitive factors necessary for cumulative learning to occur, and  
600 provides evidence of repeated bouts of elaboration and social transmission  
601 amongst the children.

602

603

Insert Figure 1 about here

604

605 In summary, at present, reports of cumulative culture in animal species  
606 remain subjective and circumstantial. Observations from the wild and captivity  
607 suggest that while some species are capable of modifying behaviour, these  
608 modifications do not seem to accrue across generations and do not clearly move  
609 beyond what individuals alone can invent for themselves (see also: Tennie et al.,  
610 2009). This suggests that while animals can transmit behaviour socially to create  
611 localized traditions, animal cultures are either not cumulative at all or  
612 cumulative in a highly restricted and simple respect.

613

## 614 **V. WHY ARE THERE DIFFERENCES IN CUMULATIVE CULTURE BETWEEN** 615 **HUMANS AND NON-HUMANS?**

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

619

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

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

625

#### 626 *(a) Cognitive differences*

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

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

631

632 *(i) Innovation:* An increased creativity, that is the ability to innovate, has been  
633 proposed to drive cumulative culture. Enquist et al. (2008) argue that cultural  
634 traits must be invented to spread within the population and be modified in a  
635 cumulative process. Whilst this argument is logical, there are extensive data  
636 documenting innovations in a range of species of primates (Reader & Laland,  
637 2002) and birds (Overington et al., 2009), yet comparatively little evidence for  
638 traditions and cumulative culture. This data suggests that innovation alone is not  
639 sufficient for cumulative culture. Indeed, a recent study suggests that innovation  
640 may act as a cultural catalyst, at least in the early stages of ratcheted  
641 technologies, functioning only to speed up the level of cultural complexity  
642 attained (Pradhan et al., 2012).

643

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

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

662         Researchers have argued that the discovery or utilisation of a more  
663 rewarding solution is suppressed by the initial discovery of a task solution  
664 (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009; Whiten et al., 2009;  
665 Hopper et al., 2011). Similar arguments concern a species propensity for  
666 functional fixedness, that is the inability to use items beyond their initially learnt  
667 affordances (Hanus et al., 2011). Specifically, it is thought that functional  
668 fixedness can occur from one's own experience with environmental features,  
669 canalising its use according to how such was personally used in the past.  
670 Alternatively, normative influence may play a role, such that one's cultural  
671 background or norms for item affordances could inhibit learning new item  
672 functions (Gruber et al., 2011; Hanus et al., 2011). According to these arguments,  
673 cumulative additions to a solution would be increasingly likely to occur in  
674 species as conservatism (and/or functional fixedness) decreased. Wood et al.  
675 (2013) have recently shown that children acquire multiple strategies to a  
676 problem, even where their first solution procured a reward of no lesser value  
677 than the alternative solutions they went on to use. Therefore, if humans are less  
678 conservative than chimpanzees, as suggested by Whiten et al. (2009), this may

679 partly explain the prevalence of cumulative culture in the former relative to the  
680 latter. However, the aforementioned study of cumulative problem solving, in  
681 children, chimpanzees and capuchin monkeys (Dean et al., 2012), found no  
682 evidence for conservatism or behavioural inflexibility in any of the species.

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

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

701

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

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

711         Recent theoretical work suggests that imitation is not necessary for non-  
712 cumulative traditions, which can emerge from simple learning processes, such as  
713 local/stimulus enhancement coupled with reinforcement learning or from  
714 asocial learning when individuals are exposed to the same environment (van der  
715 Post & Hogeweg, 2008). These learning mechanisms, while sufficient to support  
716 durable traditions (Matthews et al., 2010) or an *accumulation* of behavioural  
717 traits (van der Post & Hogeweg, 2008), would seem an insufficient foundation for  
718 cumulative culture insofar as enabling the accumulation of beneficial  
719 modifications to an existing behavioural trait, increasing its complexity. To the  
720 extent that local/stimulus enhancement results in low fidelity transmission, as is  
721 widely thought (although we note there is little hard data here), then Lewis and  
722 Laland's (In Press) theoretical analysis would not expect it to result in  
723 cumulative culture. Thus, if a species is not capable of accurate imitation (or  
724 teaching) it is much less likely that it will be able to develop cumulative culture.  
725 In support of this theory, Dean et al. (2012) found that between species  
726 (capuchins, chimpanzees and children), and within species, performance with a  
727 cumulative problem-solving task correlated strongly with the degree of task  
728 manipulations performed by individuals that matched those of their

729 predecessors at the task. It is noteworthy, however, that end state emulation can  
730 result in high-fidelity social learning and thus imitation may not be as essential  
731 for cumulative culture but rather high fidelity learning in general (Caldwell et al.,  
732 2012). However, end state emulation may result in high fidelity learning only in  
733 those tasks for which the end product can readily be recreated from viewing the  
734 action's products, while imitation is required for process-opaque tasks (Acerbi et  
735 al., 2011; Derex et al., 2012). Object movement emulation may constitute another  
736 route to high fidelity learning. For example, it has been shown that after viewing  
737 video footage of physical object movements only, through digital removal of a  
738 demonstrator's behaviour, children's object movements were comparable to  
739 when a full behavioural-object movement demonstration was viewed (Huang &  
740 Charman, 2005). Task difficulty and task demands are however likely to play an  
741 important role in whether forms of emulation are sufficient to optimise  
742 behaviour (Acerbi et al., 2011).

743         Why, then, when there is recent evidence that chimpanzees are capable of  
744 imitation (Whiten et al., 1996; Horner et al., 2006; although see Tennie et al.,  
745 2012), do they not appear to have developed cumulative culture? There are  
746 various potential explanations for this. First, while chimpanzees have shown  
747 some capacity for imitation this may be the exception rather than the rule, with  
748 other social learning mechanisms such as emulation or stimulus enhancement,  
749 associated with lower copying fidelity, responsible for much behavioural  
750 propagation (Tomasello, 1999; Tennie et al., 2009; Hopper, 2010; although see  
751 Caldwell et al., 2012). Moreover, comparative studies reveal substantive  
752 differences in the amount of imitation, and rate of imitative learning, exhibited  
753 by humans and chimpanzees (Horner & Whiten, 2005; Herrmann et al., 2007;

754 Dean et al., 2012; Hecht et al., 2012), suggesting that while chimpanzees may be  
755 capable of imitation, they are not as proficient at it (or perhaps, as motivated to  
756 imitate) as humans. Second, there is a lack of evidence that when imitating  
757 chimpanzees formulate the copied agent's intentions (Tomasello & Carpenter,  
758 2007). That is, compared to humans, chimpanzees may be less capable of  
759 rational imitation, or may be less able to imitate actions deliberately and  
760 consciously in order to achieve the same outcome as that inferred for the  
761 demonstrator. The ability to take into consideration the demonstrator's goals  
762 and intentions might plausibly facilitate cumulative culture, if this increased the  
763 accuracy of information transmission (although see arguments regarding  
764 imitation of irrelevant actions, or 'overimitation' in children (Horner & Whiten,  
765 2005; Lyons et al., 2007; Lyons et al., 2011).

766

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



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

785

786 *(v) Teaching:* Teaching is behaviour that functions to impart knowledge, and  
787 differs from other forms of social learning in requiring an active and costly  
788 investment by the tutor into the learning of the pupil (Caro & Hauser, 1992).  
789 Teaching frequently requires the teacher to infer the current knowledge state of  
790 the pupil to allow an appropriate level of support (Flynn, 2010); however,  
791 inferring knowledge states in other animals is difficult. The distribution of  
792 teaching may be wider than previously thought, with experimental evidence in  
793 meerkats, pied babblers, ants and bees (Franks & Richardson, 2006; Thornton &  
794 McAuliffe, 2006; Raihani & Ridley, 2008), although whether the teaching in non-  
795 humans is consanguineous to human teaching remains debatable (Premack,  
796 2007; Hoppitt et al., 2008). Teaching may be particularly important for the  
797 transfer of cumulative modifications, as it functions to promote the fidelity of  
798 knowledge transfer, potentially allowing specific behavioural patterns to be  
799 transmitted between individuals until such a time as beneficial modifications  
800 appear (Boyd & Richerson, 1985; Tomasello, 1999). Indeed, teaching can be  
801 characterized as behaviour that functions specifically to enhance the fidelity of  
802 information transmission. A recent mathematical analysis of the evolution of  
803 teaching (Fogarty et al., 2011) found that cumulative culture broadens the range

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

810

811 *(vi) Complex communication:* Alongside teaching, human language, a uniquely  
812 complex communication system (Tomasello, 1999; Hauser et al., 2002; Pinker &  
813 Jackendoff, 2005; Cheney & Seyfarth, 2010), may promote cumulative culture,  
814 again through facilitating accurate transmission. Language allows the  
815 transmission of intentions and complex behaviour patterns between individuals  
816 and the facilitation of easy and ‘cheap’ pedagogy; greatly enhancing teaching.  
817 Language has also enabled humans to compile written records of the beliefs,  
818 ideas, innovations and technologies of our predecessors, which provides  
819 protection against cultural loss, as well as enabling access to the knowledge of  
820 individuals that are outside individuals’ social networks. Language, both in the  
821 form of verbal and linguistic notation therefore, could enable high-fidelity  
822 transmission of modifications to existing behavioural traits, facilitating  
823 cumulative culture (Tomasello, 1999; Csibra & Gergely, 2005; Tomasello et al.,  
824 2005; Carpenter, 2006). Consistent with this, Dean et al. (2012) found that  
825 children’s performance in the cumulative task covaried with the amount of  
826 verbal instruction they received from other children.

827

828 *(vii) Prosociality:* The evolution of prosociality, enabling cooperation between  
829 individuals, increased tolerance, and the shared motivations of individuals has  
830 been proposed to support the evolution of cumulative culture (Tomasello & Call,  
831 1997; Tomasello, 1999; Tomasello et al., 2005; Tomasello & Moll, 2010). The  
832 argument states that if individuals cooperate they will be able to work on a task  
833 together, allowing naïve individuals to get closer to and thus learn from a  
834 knowledgeable individual (Tomasello & Call, 1997). Working together also  
835 allows two or more individuals to discover solutions to a task and to pool their  
836 information, thus providing the opportunity for two separate solutions to be  
837 combined or modified (Tomasello, 1999). If individuals share motivations they  
838 are able to recognise that another individual has a goal and intentions, and  
839 potentially are able to assist others to achieve their goal (Tomasello et al., 2005).  
840 Shared intentionality, in which individuals recognise that others, who may not  
841 even be present at the time, share their goals and intentions, can facilitate the  
842 modification of a behaviour pattern by many individuals, over many  
843 transmission episodes and, therefore, the evolution of cumulative culture  
844 (Tomasello et al., 2005; Tomasello & Moll, 2010). Indeed, Dean et al. (2012) also  
845 highlighted a significant role for prosocial behaviour (donation of retrieved  
846 rewards to others) in the success of children in their cumulative problem-solving  
847 task. These authors hypothesized that such prosocial behaviour signified an  
848 understanding of shared motivations and served to scaffold the learning of naïve  
849 individuals.

850 In summary, a number of cognitive differences have been proposed to  
851 explain the evolution of cumulative culture. However, it seems unlikely that one  
852 cognitive trait could explain the evolution of cumulative culture by itself. Instead

853 there may be differences in a suite of cognitive traits between species (e.g. socio-  
854 cognition: teaching, imitation, pro-social behaviour and complex communication,  
855 (Tomasello, 1999; Dean et al., 2012)), which collectively afford the high-fidelity  
856 information transmission, social tendencies, and motivations necessary for  
857 cumulative culture.

858

859 *(b) Social learning strategies*

860 Whilst social learning may often provide a cheaper and quicker method of  
861 learning than asocial learning (Rendell et al., 2010), theoretical models suggest  
862 that it should not be used indiscriminately (Boyd & Richerson, 1985; Laland,  
863 2004). Rather, to enhance fitness individuals should use social learning  
864 strategies, or cultural transmission biases, to dictate when to collect social  
865 information and from whom to acquire it (Boyd & Richerson, 1985; Laland,  
866 2004; Kendal et al., 2005; 2009b). Certain social learning strategies have been  
867 proposed to be important to the evolution of cumulative culture.

868

869 *(i) Conformity:* One such strategy is conformity, defined as the propensity to  
870 disproportionately copy the most frequent behavioural trait in the population,  
871 over and above the chance expectation (Boyd & Richerson, 1985; Henrich &  
872 Boyd, 1998; Whiten et al., 2005). Our definition of conformity differs from that  
873 deployed in social psychology, which focuses on the normative and social  
874 influence acting on the copying of (incorrect) decisions, originating from the  
875 work of Asch (1955), (Morgan & Laland, 2012). Mathematical models reveal that  
876 conformity is favoured under a very wide range of conditions (Henrich & Boyd,  
877 1998) and contributes to the high-fidelity transmission required for cumulative

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

886         Conformity, defined as copying the behaviour displayed by the majority of  
887 individuals rather than disproportionate copying of the behaviour of the  
888 majority, was recently shown in chimpanzees and 2-year-old children (Haun et  
889 al., 2012). Specifically, after observing three conspecifics demonstrate the same  
890 behaviour (each dropping a ball into a coloured box) or one individual  
891 demonstrate a different behaviour three times (drop a ball three times into a  
892 different coloured box), chimpanzees and children copied the behaviour of the  
893 majority. In contrast, orangutans showed no such majority biased copying when  
894 exposed to the same experimental procedure. While this study makes an initial  
895 step towards investigating general majority biased transmission in different  
896 primate species', the interpretation of this data is open to debate (pers. comm.  
897 Tom Morgan). As noted by Haun and colleagues (2012), further investigation in  
898 this area is needed, particularly to isolate the influence of unbiased or random  
899 copying in such tasks, as unbiased copying itself is frequency dependent. The  
900 testing of conformity bias, defined as a disproportionate likelihood of copying  
901 the most frequent trait in a population, is required before drawing conclusions  
902 on the effect conformity has on other animals' social transmission and their

903 opportunities for cumulative culture. Furthermore, avoidance of the minority  
904 response or the undemonstrated option could have played a role in the  
905 behavioural responses observed in chimpanzees and children (pers. comm. Tom  
906 Morgan). Further data will help clarify majority biased learning in these species.

907         Kandler and Laland (2009) modelled the spread of cultural traits, derived  
908 through independent innovation or cumulative modification, with different  
909 levels of conformity bias (defined as disproportionately copying the most  
910 common cultural variant) to the transmission of the traits. They found that  
911 strong conformity (in which it was difficult for frequency-independent traits to  
912 invade) tended to hinder the spread of novel innovations within the population,  
913 irrespective of whether the innovation was beneficial or not, as individuals  
914 would fail to switch to a new variant. Conversely, under a weaker conformity  
915 bias a beneficial variant could spread within the population. Some individuals  
916 would switch after determining that the new variant was more beneficial, and  
917 this was enhanced as the trait became more common by individuals using a  
918 conformist learning bias. Weak conformity was, therefore, suggested to be  
919 adaptive, since it resulted in a greater proportion of individuals adopting the  
920 beneficial variant. Such 'weak conformity' is apparently supported by the  
921 equivocal or conditional empirical evidence for conformity in humans (Coultas,  
922 2004; McElreath et al., 2005; Efferson et al., 2007; Efferson et al., 2008;  
923 McElreath et al., 2008; Eriksson & Coultas, 2009; Morgan et al., 2012). Thus the  
924 impact of conformity, and, indeed, the extent to which species do conform, is  
925 currently unclear.

926

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

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

936

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

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

953 The participants also used (conditional) proportional imitation strategies,  
954 whereby individuals copy the behaviour of others in proportion to how much  
955 better the other's payoff is than their own (Schlag, 1998). Game theory analysis  
956 has established that this strategy optimises cumulative cultural learning (Schlag,  
957 1998).

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

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



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

985

986 *(c) Social structure*

987 In humans, differences in population size, connectedness and social structure are  
988 thought to alter the ease with which complex behaviour patterns can be  
989 transmitted between individuals, thus accounting for the observed distribution  
990 of cumulative culture (Powell et al., 2009; Kline & Boyd, 2010; Hill et al., 2011).  
991 In animals, social structure is normally measured by factors such as the  
992 dominance gradient (the ability of low-ranking individuals to win fights with  
993 higher-ranking individuals), amount of social play, the intensity of aggression  
994 within populations and the frequency of conciliatory displays (Thierry et al.,  
995 2008). In species with a steep dominance gradient, social factors may hinder the  
996 invention and spread of cumulative modifications. A recent mathematical model  
997 of cultural progression found that increasing the number of tolerant  
998 knowledgeable individuals, is expected to generate higher levels of technological  
999 complexity, with tolerance thought to be essential in the initial stages of cultural  
1000 progression (Pradhan et al., 2012). Thus, social structure may account for some  
1001 variation in the extent of cumulative culture (Burkart & van Schaik, 2010; Coussi-  
1002 Korbel & Frigaszy, 1995).

1003 (i) *Monopolisation*: By monopolising resources and scrounging from low-rankers,  
1004 dominant individuals may exploit those lower in the social hierarchy and  
1005 prevent them from accessing novel resources (Lavallee, 1999; Soma & Hasegawa,  
1006 2004). In an experiment investigating tool use in free-ranging captive brown  
1007 capuchins (*Cebus apella*), Lavallee (1999) reported that the alpha male would  
1008 frequently chase low-ranking individuals away from the tree stump that  
1009 contained resources of honey. Out of a group of 11 individuals, four never had  
1010 the opportunity to interact with the task and others were also constrained in the  
1011 amount of time they could spend at the resource. Similar findings have been  
1012 reported in a study of social learning in wild lemurs (*Lemur catta*, Kendal et al.,  
1013 2010a). In a review of the primate literature, Reader and Laland (2001) found  
1014 that there were more reports of innovations in low-ranking individuals than  
1015 high- or mid-ranking individuals. If low-ranking individuals have a greater  
1016 propensity to innovate than high-ranking individuals but, because of the  
1017 activities of dominants, experience restricted opportunities to interact with  
1018 novel resources, or to perform any innovative behaviour they devise, then  
1019 innovation may be curtailed. This, coupled with the reported decreased  
1020 likelihood of individuals observing novel behaviour by low rankers compared to  
1021 high rankers (Coussi-Korbel & Fragaszy, 1995; Kendal et al., In prep), means that  
1022 the population may not be able to exhibit cumulative social learning.

1023

1024 (ii) *Scrounging*: Several studies have reported a relationship between the level of  
1025 scrounging, or kleptoparasitism, that individuals commit and the amount that  
1026 they learn socially (Giraldeau & Lefebvre, 1987; Beauchamp & Kacelnik, 1991;  
1027 Lefebvre & Helder, 1997; Midford et al., 2000; Caldwell & Whiten, 2003),

1028 although the direction of this relationship varies. Some studies have found that  
1029 social learning was inhibited by scrounging (Giraldeau & Lefebvre, 1987;  
1030 Lefebvre & Helder, 1997), leading to the hypothesis that, when able to scrounge,  
1031 individuals do not learn cues about the task from the demonstrator, but rather  
1032 learn that the demonstrator itself is a source of food (Giraldeau & Lefebvre,  
1033 1987; Beauchamp & Kacelnik, 1991). Scrounging, by inhibiting learning about  
1034 the task itself, might therefore restrict the spread of social information, thereby  
1035 hindering cumulative culture.

1036         However, other researchers have found that scrounging enhanced the  
1037 learning of observers regarding a novel extractive foraging puzzle box (Midford  
1038 et al., 2000; Caldwell & Whiten, 2003). In these studies animals able to scrounge  
1039 performed better when given the opportunity to interact with the novel task,  
1040 than those that were not permitted to scrounge. The researchers argue that  
1041 scrounging promoted closer observation of the novel behaviour pattern and  
1042 attendance to cues of the puzzle box, rather than simply associating the  
1043 demonstrator with food, which allowed the scrounger to learn a behaviour  
1044 pattern more efficiently (Caldwell & Whiten, 2003).

1045         Social learning may also depend upon species' social tolerance levels  
1046 (Fragaszy & Visalberghi, 1989; Coussi-Korbel & Fragaszy, 1995; Caldwell &  
1047 Whiten, 2003). Animals that display greater social tolerance of one another  
1048 (more egalitarian species) may exhibit enhanced social learning with scrounging,  
1049 since the co-action and close proximity allows the observers to learn from the  
1050 demonstrator more effectively. In contrast, scrounging may have an inhibitory  
1051 effect on social learning in despotic animals (displaying lower social tolerance)  
1052 due to a reduction in the opportunity for coaction and subsequent ability of

1053 dominant individuals to access the resources (Coussi-Korbel & Frigaszy, 1995).  
1054 An important contributing factor in the development of cumulative culture, thus,  
1055 may be a species' level of social tolerance, with species displaying high social  
1056 tolerance, such as *Homo sapiens*, able to transfer more complex information.  
1057 However, since cumulative culture is not found in all egalitarian species, and a  
1058 lack of social tolerance was not found to contribute to a lack of cumulative  
1059 culture in chimpanzees or capuchins (Dean et al., 2012) factors other than social  
1060 tolerance must also contribute to its evolution.

1061

#### 1062 *(d) Demography*

1063 Demographic factors have also been proposed to influence cumulative  
1064 culture. Powell et al. (2009; 2010) have proposed that the changes in human  
1065 culture during the late Pleistocene, observed in the archaeological record, are  
1066 explained by demographic factors. Using simulation models building on a model  
1067 of Henrich's (2004), Powell et al (2009; 2010) found that high population  
1068 densities and high migration rates between subpopulations resulted in  
1069 accumulation of modifications and increased complexity in technologies (see  
1070 also Kline & Boyd, 2010). They hypothesise that population dynamics may have  
1071 played an important part in the acceleration of cumulative cultural change  
1072 around 50 kya. However, a key assumption of the models is the pre-existence of  
1073 the cognitive capacities for social learning and cumulative culture in humans,  
1074 therefore, clearly demography alone is insufficient to generate cumulative  
1075 culture without these cognitive capabilities. Hill et al. (2011) highlight various  
1076 hunter gatherer group composition properties unique among the primates that  
1077 may have implications for the emergence of cumulative culture. These include

1078 hunter gatherer bands being composed of a large proportion of non-kin  
1079 (suggesting cooperation between unrelated individuals), flexible patterns of  
1080 male and/or female dispersal, maintained lifelong social bonds (Chapais, 2011;  
1081 Rodseth et al., 1991) and bands forming constituent parts of larger social  
1082 networks. A likely by-product of these group structures is pronounced social  
1083 transmission and continued flow of cultural practices, knowledge and ideas  
1084 between bands and sub-populations, accentuating the probability that traits will  
1085 accumulate within and across populations. In contrast, for chimpanzees,  
1086 (affiliative) contact between communities is composed almost exclusively of  
1087 female migration, upon which contact with the natal group is lost (Chapais,  
1088 2011). Thus we see that human band compositions are especially well suited to  
1089 cultural transmission on a large scale. As such, a species' demography may play  
1090 an important role in whether or not their culture has accumulated over  
1091 generations.

1092         Enquist et al. (2010) investigated how the number of animals an  
1093 individual is able to copy affects the persistence of a cultural trait over time. They  
1094 used mathematical models to investigate under what conditions copying a single  
1095 cultural 'parent' could support a stable culture. They found that multiple cultural  
1096 parents were typically necessary for a stable culture as, unless perfect  
1097 transmission was possible, then copying of single cultural parents would result  
1098 in the proportion of individuals expressing a trait decreasing generation after  
1099 generation. This suggests that a population with overlapping generations and the  
1100 opportunity for learning from multiple individuals promotes cultural  
1101 transmission.

1102           Whilst a larger population size has a positive effect on the development  
1103 and sustainability of complex cumulative culture, small, isolated populations may  
1104 also lose cultural complexity. The best known example of cultural loss is the  
1105 island of Tasmania, where humans arrived about 34 kya and were isolated from  
1106 the mainland between 12 kya and 10 kya (Henrich, 2004). Subsequently, the  
1107 Tasmanians lost all but 24 items in their toolkit, compared to a toolkit of  
1108 hundreds on mainland Australia. Thus, when Europeans arrived in the 18<sup>th</sup>  
1109 century there was no bone technology, no skills for making winter clothing and  
1110 no ability to fish as seen in mainland Australian aborigine populations (Henrich,  
1111 2004). In modelling the data Henrich found that as population size dropped it  
1112 became much easier for losses of behavioural traits to occur due to small copying  
1113 errors. The isolation of Tasmania meant that the small population could rapidly  
1114 lose technologies, with little chance of innovations from within their population  
1115 or from migrant individuals.

1116           The Tasmanian example is replicated with other populations in the Pacific  
1117 Ocean. Kline and Boyd (2010) found that in Pacific islands the population size  
1118 and rate of contact with other populations correlated with the complexity of the  
1119 marine foraging technology. Whilst acknowledging that complex technologies  
1120 may increase the carrying capacity of the population, the authors speculate that  
1121 the influx of migrant ideas and range of ideas from a larger population allow  
1122 modifications to cultural traits to be made more rapidly, ratcheting up  
1123 complexity.

1124           In summary, the size, network structure and mobility of populations may  
1125 impact upon the number of cultural traits that a population can sustain. Clearly  
1126 demography alone cannot account for the initial development of individual

1127 cumulative cultural traits, otherwise it would be widespread in nature. However,  
1128 population size will influence the speed at which technologies ratchet up in  
1129 complexity, and the level of diversity maintained (Pradhan et al., 2012).

1130

## 1131 **(2) Efficiencies and complexities**

1132 Throughout this review, there has been discussion of empirical work and  
1133 field observations that focus on an increase in complexity over time. The ratchet  
1134 effect, as originally described by Tomasello (1994), specifically referred to  
1135 increases in complexity with social transmission. This increase in complexity is  
1136 hypothesised to have created the many artefacts, institutions and complex  
1137 technologies that humans display across populations (Tomasello, 1999).

1138 However, we wish to emphasise that in cumulative culture, combined  
1139 with complexity, there must also be changes in efficiency. It is likely that cultural  
1140 traits that simply become more complex, with no improvements in efficiency,  
1141 would simply become too complex for individuals to learn or gain sufficient  
1142 benefit to justify learning them. For example, Mesoudi (2011b) has posited a  
1143 limit to cumulative complexity due to the costs of acquiring a complex trait from  
1144 the previous generation within a life-time. An obvious example of the proposed  
1145 requirement for improved efficiency alongside complexity is that of computing  
1146 technology; computers, have become more compact, and user friendly, as they  
1147 have become more powerful.

1148 Some studies featured in this review have solely focussed on cumulative  
1149 improvements in efficiency (Flynn, 2008; Kirby et al., 2008). Flynn (2008) finds  
1150 that the imitation of causally irrelevant actions, (or 'over-imitation'), as seen in  
1151 other experiments with humans (Horner & Whiten, 2005; Nielsen & Tomaselli,

1152 2010; Wood et al., 2012) reduces over laboratory generations with children  
1153 employing rational rather than blind/faithful imitation, making the technique  
1154 used to solve the task more efficient. Similarly, the decrease in diversity, and thus  
1155 increase in efficiency, of Kirby et al.'s (2008) artificial languages, relies on  
1156 mistakes made by individuals. Indeed, the structured manner in which  
1157 individuals made language learning 'mistakes' resulted in the structure that  
1158 emerged in the language, in turn enabling efficient language learning.

1159 To take an alternative example, New Caledonian Crows are observed to  
1160 make a variety of different hooked tools (Hunt & Grey, 2003). However, Sanz et  
1161 al (2009) assert that these hooks do not enhance the efficiency with which the  
1162 crows can gain food, they are simply additions to the tool which increase its  
1163 physical complexity. We see this as an empirical issue: if evidence can be  
1164 provided that step tools are more efficient than other tools then (provided these  
1165 tools also meet the other criteria outlined in Table 1) they may yet prove to be a  
1166 case of cumulative culture. Likewise, we may posit a similar argument for the  
1167 stone-handling of Japanese macaques which may increase in complexity yet, as  
1168 there is no apparent 'purpose' to the behaviour, does not increase efficiency.  
1169 Finally, there are examples in human culture in which ceremonial or decorative  
1170 items become more complex to manufacture, independent of their original  
1171 function (functioning instead, for example, as signs of wealth, position, skill or  
1172 power) and thus without increases in the efficiency with which a target is  
1173 achieved (Basalla, 1988). For example, the Torres Strait culture created ornate  
1174 decorative (turtle shell) fish hook ornaments that were worn by married women  
1175 (Hedley, 1907, cited by Florek, 2005), creating complex, carved, symbolic  
1176 cultural artefacts that did not increase the efficiency of the items' original fishing



1177 function (although the efficiency with which it acted as a display could be  
1178 investigated).

1179         We emphasise that whilst cumulative culture primarily drives the  
1180 complexity of cultural traits, the efficiency with which the trait is transmitted,  
1181 executed, and enables achievement of its intended purpose, may also change.  
1182 Thus the interplay between the complexity and efficiency of cumulative cultural  
1183 traits potentially influences how traits evolve with some showing increasing  
1184 efficiency and reducing complexity (e.g. language change in the laboratory),  
1185 some increasing complexity and increasing efficiency (e.g. computing  
1186 technology) and others increasing in complexity and reducing in efficiency (e.g.  
1187 symbolic culture). We believe that this is a neglected aspect of research into  
1188 cumulative culture, which warrants further investigation.

1189

1190

## 1191 **VI. CONCLUSIONS**

1192         (i)     Historical evidence suggests that human culture is cumulative, with  
1193                 successive generations building on what went before. This evidence is  
1194                 supported by empirical data, which suggests that humans are able to  
1195                 observe other individuals and modify what they have seen.

1196         (ii)    Although some researchers have argued that certain non-human  
1197                 species ratchet up the complexity of cultural traits, the evidence that  
1198                 non-humans have cumulative culture is weak. Presently there is no  
1199                 evidence that any species, except humans, have cumulative culture.

1200                 Some evidence from the wild suggests that modifications have been

1201 made to the behavioural traits of some animals, but evidence that  
1202 these were socially transmitted is lacking.

1203 (iii) There have been a number of different hypotheses advanced for the  
1204 evolution of cumulative culture. Current evidence supports the view  
1205 that a package of sociocognitive capabilities (including teaching,  
1206 imitation, verbal instruction and prosocial tendencies) present in  
1207 humans, but not other animals, underpins cumulative cultural  
1208 learning, probably because it promotes high-fidelity information  
1209 transmission.

1210 (iv) Currently, studies of cumulative culture often focus solely on increases  
1211 in trait complexity. However, evidence from historical reports and  
1212 experimental investigation suggest that there are also associated  
1213 changes in trait efficiency, which warrant investigation.

1214

### 1215 **Acknowledgements**

1216 LGD was supported by an EU-Nestpathfinder grant (043434FP6-2004-  
1217 NESTPATH) to KNL, GV by a Durham University Social and Health  
1218 Interdisciplinary Scholarship, KNL by an Advanced grant (EVOCULTURE  
1219 232823), EGF by an ESRC Grant, and RLK by a Royal Society Dorothy Hodgkin  
1220 Fellowship. We appreciate helpful discussions with Jamie Tehrani, Jeremy  
1221 Kendal and Tom Morgan.

1222

- 1223 (2005). So much more to know. — In: *Science*, p. 78-102.
- 1224 ACERBI, A., TENNIE, C. & NUNN, C. (2011). Modeling imitation and emulation in  
1225 constrained search spaces. — *Learning & Behavior* 39, 104-114.
- 1226 ASCH, S. E. (1955). Opinions and Social Pressure. — *Scientific American* 193, 31-  
1227 35.
- 1228 BASALLA, G. (1988). *The Evolution of Technology*. — Cambridge University Press,  
1229 Cambridge.
- 1230 BEAUCHAMP, G. & KACELNIK, A. (1991). Effects of the knowledge of partners on  
1231 learning rates in zebra finches *Taeniopygia guttata*. — *Animal Behaviour*  
1232 41, 247-253.
- 1233 BOESCH, C. (2003). Is culture a golden barrier between human and chimpanzee?  
1234 — *Evolutionary Anthropology* 12, 82-91.
- 1235 BOESCH, C., HEAD, J. & ROBBINS, M. M. (2009). Complex tool sets for honey  
1236 extraction among chimpanzees in Loango National Park, Gabon. —  
1237 *Journal of Human Evolution* 56, 560-569.
- 1238 BOYD, R. & RICHERSON, P. (1985). *Culture and the Evolutionary Process*. — Chicago  
1239 University Press, Chicago.
- 1240 BOYD, R. & RICHERSON, P. J. (1996). Why Culture is Common, but Cultural Evolution  
1241 is Rare. — *Proceedings of the British Academy* 88, 77-93.
- 1242 BURKART, J.M. & VAN SCHAIK, C.P. (2010). Cognitive consequences of cooperative  
1243 breeding in primates? — *Animal Cognition* 13: 1-19
- 1244 CALDWELL, C. & MILLEN, A. (2008). Experimental models for testing hypotheses  
1245 about cumulative cultural evolution. — *Evolution and Human Behavior*  
1246 29, 165-171.
- 1247 CALDWELL, C. A. & MILLEN, A. E. (2009). Social Learning Mechanism and Cumulative  
1248 Cultural Evolution. — *Psychological Science* 20, 1478-1487.
- 1249 —. (2010a). Conservatism in laboratory microsocieties: unpredictable payoffs  
1250 accentuate group-specific traditions. — *Evolution and Human Behavior*  
1251 31, 123-130.
- 1252 —. (2010b). Human cumulative culture in the laboratory: Effects of (micro)  
1253 population size. — *Learning and Behavior* 38, 310-318.
- 1254 CALDWELL, C. A., SCHILLINGER, K., EVANS, C. L. & HOPPER, L. M. (2012). End State  
1255 Copying by Humans (*Homo sapiens*): Implications for a Comparative  
1256 Perspective on Cumulative Culture. — *Journal of Comparative Psychology*  
1257 126, 161-169.
- 1258 CALDWELL, C. A. & WHITEN, A. (2003). Scrounging facilitates social learning in  
1259 common marmosets, *Callithrix jacchus*. — *Animal Behaviour* 65, 1085-  
1260 1092.
- 1261 CARO, T. & HAUSER, M. (1992). Is there teaching in nonhuman animals? —  
1262 *Quarterly Review of Biology* 67, 151-174.
- 1263 CARPENTER, M. (2006). Instrumental, Social, and Shared Goals and Intentions in  
1264 Imitation. — In: *Imitation and the Social Mind. Autism and Typical*  
1265 *Development* (S. J. Rogers & J. H. G. Williams, eds). The Guilford Press,  
1266 London.
- 1267 CARPENTER, M., AKHTAR, N. & TOMASELLO, M. (1998). Fourteen- to 18-month old  
1268 infants differentially imitate intentional and accidental actions. — *Infant*  
1269 *Behavior and Development* 21, 315-330.
- 1270 CAVALLI-SFORZA, L. & FELDMAN, M. (1981). *Cultural Transmission and Evolution: A*  
1271 *Quantitative Approach*. — Princeton University Press, Princeton, NJ.

- 1272 CHENEY, D. L. & SEYFARTH, R. M. (2010). Primate Communication and Human  
1273 Language: Continuities and Discontinuities —In: *Mind the Gap: Tracing*  
1274 *the Origins of Human Universals* (P. M. Kappeler & J. B. Silk, eds).  
1275 Springer, Berlin.
- 1276 COULTAS, J. C. (2004). When in Rome... And evolutionary perspective on  
1277 conformity. — *Processes & Intergroup Relations* 7, 317-331.
- 1278 COUSSI-KORBEL, S. & FRAGASZY, D. M. (1995). On the relation between social  
1279 dynamics and social learning. — *Animal Behaviour* 50, 1441-1453.
- 1280 CSIBRA, G. & GERGELY, G. (2005). Social learning and social cognition: The case for  
1281 pedagogy. — In: *Processes of Change in Brain and Cognitive Development.*  
1282 *Attention and Performance* (Y. Munakata & M. H. Johnson, eds). Oxford  
1283 University Press, Oxford, p. 249-274.
- 1284 D'ANDRADE, R. (2008). Some Kinds of Causal Powers That Make Up Culture. — In:  
1285 *Explaining Culture Scientifically* (M. J. Brown, ed). University of  
1286 Washington Press, London.
- 1287 DEAN, L. G., KENDAL, R. L., SCHAPIRO, S. J., THIERRY, B. & LALAND, K. N. (2012).  
1288 Identification of the Social and Cognitive Processes Underlying Human  
1289 Cumulative Culture. — *Science* 335, 1114-1118.
- 1290 DEREX, M., GODELLE, B. & RAYMOND, M. (2012). Social learners require process  
1291 information to outperform individual learners. — *Evolution*, 67, 688-97.
- 1292 EFFERSON, C., LALIVE, R., RICHERSON, P., MCELREATH, R. & LUBELL, M. (2008).  
1293 Conformists and mavericks: the empirics of frequency-dependent cultural  
1294 transmission. — *Evolution and Human Behavior* 29, 56-64.
- 1295 EFFERSON, C., RICHERSON, P. J., MCELREATH, R., LUBELL, M., EDSTEN, E., WARING, T. M.,  
1296 PACIOTTI, B. & BAUM, W. (2007). Learning, productivity and noise: an  
1297 experimental study of cultural transmission on the Bolivian Altiplano. —  
1298 *Evolution and Human Behavior* 28, 11-17.
- 1299 EHN, M. & LALAND, K. N. (2012). Adaptive strategies for cumulative cultural  
1300 learning. — *Journal of Theoretical Biology* 301, 103-111.
- 1301 ENQUIST, M. & GHIRLANDA, S. (2007). Evolution of social learning does not explain  
1302 the origin of human cumulative culture. — *Journal of Theoretical Biology*  
1303 246, 129-135.
- 1304 ENQUIST, M., GHIRLANDA, S., JARRICK, A. & WACHTMEISTER, C.-A. (2008). Why does  
1305 human culture increase exponentially? — *Theoretical Population Biology*  
1306 74, 46-55.
- 1307 ENQUIST, M., STRIMLING, P., ERIKSSON, K., LALAND, K. & SJOSTRAND, J. (2010). One  
1308 cultural parent makes no cultural —*Animal Behaviour* 79, 1353-1362.
- 1309 ERIKSSON, K. & COULTAS, J. C. (2009). Are people really conformist-biased? An  
1310 empirical test and a new mathematical model. — *Journal of Evolutionary*  
1311 *Psychology* 7, 5-21.
- 1312 ERIKSSON, K., ENQUIST, M. & GHIRLANDA, S. (2007). Critical points in current theory  
1313 of conformist social learning. — *Journal of Evolutionary Psychology* 5, 67-  
1314 87.
- 1315 FLOREK, S. (2005). The Torres Strait Islands collection at the Australian Museum. -  
1316 - *Technical Reports of the Australian Museum* 19, 1-19.
- 1317 FLYNN, E. (2008). Investigating children as cultural magnets: do young children  
1318 transmit redundant information along diffusion chains? — *Philosophical*  
1319 *Transactions of the Royal Society B: Biological Sciences* 363, 3541-3551.

- 1320 —. (2010). Underpinning Collaborative Learning. — In: Self and Social  
1321 Regulation: Social interaction and the development of social  
1322 understanding and executive functions (B. Sokol, U. Muller, J. Carpendale,  
1323 A. Young & G. Iarocci, eds). Oxford University Press, Oxford, p. 312-336.
- 1324 FOGARTY, L., STRIMLING, P. & LALAND, K. N. (2011). The evolution of teaching. —  
1325 Evolution 65, 2760-2770.
- 1326 FRAGASZY, D. M. & VISALBERGHI, E. (1989). Social influences on the acquisition and  
1327 use of tools in tufted capuchin monkeys (*Cebus apella*). — Journal of  
1328 Comparative Psychology 103, 159-170.
- 1329 FRANKS, N. & RICHARDSON, T. (2006). Teaching in tandem-running ants. — Nature  
1330 439, 153-153.
- 1331 GALEF, B. G. (1992). The Question of Animal Culture. — Human Nature 3, 157-  
1332 178.
- 1333 GALEF JR, B. G., DUDLEY, K. E. & WHISKIN, E. E. (2008). Social learning of food  
1334 preferences in dissatisfied and uncertain rats. — Animal behaviour 75,  
1335 631-637.
- 1336 GERGELY, G., BEKKERING, H. & KIRALY, I. (2002). Rational imitation in preverbal  
1337 infants. — Nature 415, 755.
- 1338 GIRALDEAU, L. & LEFEBVRE, L. (1987). Scrounging prevents cultural transmission of  
1339 food-finding behaviour in pigeons. — Animal Behaviour 35, 387-394.
- 1340 GRUBER, T., MULLER, M. N., REYNOLDS, V., WRANGHAM, R. & ZUBERBUHLER, K. (2011).  
1341 Community-specific evaluation of tool affordances in wild chimpanzees.  
1342 — Sci. Rep. 1.
- 1343 HANUS, D., MENDES, N., TENNIE, C. & CALL, J. (2011). Comparing the Performances of  
1344 Apes (*Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*) and Human  
1345 Children (*Homo sapiens*) in the Floating Peanut Task. — PLoS ONE 6,  
1346 e19555.
- 1347 HAUN, D. B. M., REKERS, Y. & TOMASELLO, M. (2012). Majority-Biased Transmission  
1348 in Chimpanzees and Human Children, but Not Orangutans. — Current  
1349 Biology 22, 727-731.
- 1350 HAUSER, M. D., CHOMSKY, N. & FITCH, W. T. (2002). The faculty of language: What is  
1351 it, who has it, and how did it evolve? — Science 298, 1569-1579.
- 1352 HECHT, E. E., PATTERSON, R. & BARBEY, A. K. (2012). What can other animals tell us  
1353 about human social cognition? An evolutionary perspective on reflective  
1354 and reflexive processing. — Frontiers in Human Neuroscience 6.
- 1355 HELFMAN, G. S. & SCHULTZ, E. T. (1984). Social traditions of behavioral traditions in  
1356 a coral reef fish. — Animal Behaviour 32, 379-384.
- 1357 HENRICH, J. (2004). Demography and cultural evolution: how adaptive cultural  
1358 processes can produce maladaptive losses: the Tasmanian case. —  
1359 American Antiquity 69, 197-214.
- 1360 HENRICH, J. & BOYD, R. (1998). The evolution of conformist transmission and the  
1361 emergence of between-group differences. — Evolution and Human  
1362 Behavior 19, 215-241.
- 1363 HERRMANN, E., CALL, J., HERNANDEZ-LLOREDA, M., HARE, B. & TOMASELLO, M. (2007).  
1364 Humans Have Evolved Specialized Skills of Social Cognition: The Cultural  
1365 Intelligence Hypothesis. — Science 317, 1360-1366.
- 1366 HEYES, C. (1993). Imitation, culture and cognition. — Animal Behaviour 46, 999-  
1367 1010.

- 1368 HILL, K. R., WALKER, R. S., BOZICEVIC, M., EDER, J., HEADLAND, T., HEWLETT, B., HURTADO,  
1369 A. M., MARLOWE, F., WIESSNER, P. & WOOD, B. (2011). Co-residence patterns  
1370 in hunter-gatherer societies show unique human social structure. —  
1371 Science 331, 1286- 1289.
- 1372 HOLZHAIDER, J. C., HUNT, G. R. & GRAY, R. D. (2010). Social Learning in New  
1373 Caledonian crows. — Learning and Behavior 38, 206-219.
- 1374 HOPPER, L. M. (2010). 'Ghost' experiments and the dissection of social learning in  
1375 humans and animals. — Biological Reviews 85, 685-701.
- 1376 HOPPER, L. M., SCHAPIRO, S. J., LAMBETH, S. P. & BROSNAN, S. F. (2011). Chimpanzees'  
1377 socially maintained food preferences indicate both conservatism and  
1378 conformity. — Animal Behaviour 81, 1195-1202.
- 1379 HOPPITT, W. J. E., BROWN, G. R., KENDAL, R., RENDELL, L., THORNTON, A., WEBSTER, M. M.  
1380 & LALAND, K. N. (2008). Lessons from animal teaching. — Trends in  
1381 Ecology & Evolution 23, 486-493.
- 1382 HORNER, V. & WHITEN, A. (2005). Causal knowledge and imitation/emulation  
1383 switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*).  
1384 — Animal Cognition 8, 164-181.
- 1385 HORNER, V., WHITEN, A., FLYNN, E. & DE WAAL, F. (2006). Faithful replication of  
1386 foraging techniques along cultural transmission chains by chimpanzees  
1387 and children. — Proceedings of the National Academy of Sciences 103,  
1388 13878-13883.
- 1389 HRUBESCH, C., PREUSCHOF, S. & VAN SCHAIK, C. (2009). Skill mastery inhibits  
1390 adoption of observed alternative solutions among chimpanzees (*Pan*  
1391 *troglodytes*). — Animal Cognition 12, 209-216.
- 1392 HUANG, C.-T. & CHARMAN, T. (2005). Gradations of emulation learning in infants  
1393 imitation of actions on objects. — Journal of Experimental Child  
1394 Psychology 92, 276-302.
- 1395 HUFFMAN, M., NAHALLAGE, C. & LECA, J. (2008). Cultured Monkeys: Social Learning  
1396 Cast in Stones. — Current Directions in Psychological Science 17, 410-  
1397 414.
- 1398 HUMLE, T. & MATSUZAWA, T. (2002). Ant-Dipping Among the Chimpanzees of  
1399 Bossou, Guinea, and Some Comparisons With Other Sites. — American  
1400 Journal of Primatology 58, 133-148.
- 1401 HUNT, G. & GRAY, R. (2003). Diversification and cumulative evolution in New  
1402 Caledonian crow tool manufacture. — Proceedings of the Royal Society B:  
1403 Biological Sciences 270, 867-874.
- 1404 —. (2004). The crafting of hook tools by wild New Caledonian crows. —  
1405 Proceedings of the Royal Society B: Biological Sciences 271, S88-S90.
- 1406 KANDLER, A. & LALAND, K. N. (2009). An investigation of the relationship between  
1407 innovation and cultural diversity. — Theoretical Population Biology 76,  
1408 59-67.
- 1409 KENDAL, J., RENDELL, L. R., PIKE, T. W. & LALAND, K. N. (2009a). Nine-spined  
1410 sticklebacks employ a hill-climbing social learning strategy. —  
1411 Behavioural Ecology 20, 238-244.
- 1412 KENDAL, R., COE, R. & LALAND, K. (2005). Age differences in neophilia, exploration,  
1413 and innovation in family groups of callitrichid monkeys. — American  
1414 Journal of Primatology 66, 167-188.

- 1415 KENDAL, R., KENDAL, J., HOPPITT, W. & LALAND, K. (2009b). Identifying Social  
1416 Learning in Animal Populations: A New 'Option-Bias' Method. — *PLoS*  
1417 *One* 4, e6541.
- 1418 KENDAL, R. L., CUSTANCE, D. M., KENDAL, J. R., VALE, G., STOINKSI, T. S., RAKOTOMALALA, N.  
1419 L. & RASAMIMANA, H. (2010a). Evidence for social learning in wild lemurs  
1420 (*Lemur catta*). — *Learning and Behavior* 38, 220-234.
- 1421 KENDAL, R. L., GALEF JR, B. G. & VAN SCHAIK, C. P., eds. (2010b). Capturing Social  
1422 Learning in Natural Contexts: Methodological Insights and Implications  
1423 for Culture. —
- 1424 KENDAL, R. L., HOPPER, L. M., BROSNAN, S. F., SCHAPIRO, S. J., LAMBETH, S. & HOPPITT, W.  
1425 (In prep). Transmission biases in chimpanzees. —
- 1426 KENWARD, B., RUTZ, C., WEIR, A. A. S. & KACELNIK, A. (2006). Development of tool use  
1427 in New Caledonian crows: inherited action patterns and social influence.  
1428 — *Animal Behaviour* 72, 1329-1343.
- 1429 KENWARD, B., WEIR, A. A. S., RUTZ, C. & KACELNIK, A. (2005). Tool manufacture by  
1430 naive juvenile crows. — *Nature* 433, 121.
- 1431 KIRBY, S., CORNISH, H. & SMITH, K. (2008). Cumulative Cultural Evolution in the Lab:  
1432 an experimental approach to the origins of structure in human language.  
1433 — *Proceedings of the National Academy of Science* 105, 10681-10686.
- 1434 KLINE, M. A. & BOYD, R. (2010). Population size predicts technological complexity  
1435 in Oceania. — *Proceedings of the Royal Society B: Biological Sciences* 277,  
1436 2559-2564.
- 1437 KROEBER, A. L. & KLUCKHORN, C. (1952). *Culture: A Critical Review of Concepts and*  
1438 *Definitions*. — Harvard University Press, Cambridge, MA.
- 1439 LALAND, K. (2004). Social learning strategies. — *Learning and Behavior* 32, 4-14.
- 1440 LALAND, K. N. & GALEF, B. G. (2009). *The Question of Animal Culture*. — Harvard  
1441 University Press, Cambridge.
- 1442 LALAND, K. N. & HOPPITT, W. (2003). Do animals have culture? — *Evolutionary*  
1443 *Anthropology* 12, 150-159.
- 1444 LALAND, K. N. & JANIK, V. M. (2006). The animal culture debate. — *Trends in*  
1445 *Ecology & Evolution* 21, 542-547.
- 1446 LALAND, K. N., KENDAL, J. R. & KENDAL, R. L. (2009). *Animal Culture: Problems and*  
1447 *Solutions*. — In: *The Question of Animal Culture* (K. N. Laland & B. G.  
1448 Galef, eds). Harvard University Press, Cambridge, Massachusetts, p. 174-  
1449 197.
- 1450 LAVALLEE, A. C. (1999). Capuchin (*Cebus apella*) tool use in a captive naturalistic  
1451 environment. — *International Journal of Primatology* 20, 399-414.
- 1452 LECA, J.-B., GUNST, N. & HUFFMAN, M. A. (2010). Indirect social influence in the  
1453 maintenance of the stone-handling tradition in Japanese macaques,  
1454 *Macaca fuscata*. — *Animal Behaviour* 79, 117-126.
- 1455 LECA, J., GUNST, N. & HUFFMAN, M. (2007). Japanese macaque cultures: inter-and  
1456 intra-troop behavioural variability of stone handling patterns across 10  
1457 troops. — *Behaviour* 144, 251-281.
- 1458 LEFEBVRE, L. & HELDER, R. (1997). Scrounger numbers and the inhibition of social  
1459 learning in pigeons. — *Behavioural Processes* 40, 201-207.
- 1460 LEFEBVRE, L. & PALAMETA, B. (1988). Mechanisms, Ecology, And Population  
1461 Diffusion of Socially-Learned Food-Finding Behaviour in Feral Pigeons. —  
1462 In: *Social Learning. Psychological and Biological Perspectives* (T. Zentall &  
1463 B. G. Galef, eds). Lawrence Erlbaum Associates, Hillsdale, NJ.

- 1464 LEHMAN, H. (1947). The exponential increase of man's cultural output. — Social  
1465 Forces, 281-290.
- 1466 LEHNER, S. R., BURKHART, J. M. & VAN SCHAİK, C. P. (2011). Can captive orangutans  
1467 (*Pongo pygmaeus abelli*) be coaxed into cumulative build-up of  
1468 techniques? — Journal of Comparative Psychology 125, 446-455.
- 1469 LEWIS, H. M. & LALAND, K. N. (In Press). Transmission fidelity is the key to the  
1470 build-up of cumulative culture. — Philosophical Transactions of the Royal  
1471 Society B.
- 1472 LUMSDEN, C. J. & WILSON, E. O. (1981). Genes, Mind and Culture: The  
1473 Coevolutionary Process. — Harvard University Press, Cambridge.
- 1474 LYONS, D. E., DAMROSCH, D. H., LIN, J. K., MACRIS, D. M. & KEIL, F. C. (2011). The scope  
1475 and limits of overimitation in the transmission of artefact culture. —  
1476 Philosophical Transactions of the Royal Society B: Biological Sciences 366,  
1477 1158-1167.
- 1478 LYONS, D. E., YOUNG, A. G. & KEIL, F. C. (2007). The hidden structure of  
1479 overimitation. — Proceedings of the National Academy of Sciences 104,  
1480 19751-19756.
- 1481 MARSHALL-PESCINI, S. & WHITEN, A. (2008). Chimpanzees (*Pan troglodytes*) and the  
1482 question of cumulative culture: an experimental approach. — Animal  
1483 Cognition 11, 449-456.
- 1484 MATTHEWS, L. J., PAUKNER, A. & SUOMI, S. J. (2010). Can traditions emerge from the  
1485 interaction of stimulus enhancement and reinforcement learning? An  
1486 experimental model. — American Anthropologist 112, 257-269.
- 1487 MCELREATH, R., BELL, A., EFFERSON, C., LUBELL, M., RICHERSON, P. & WARING, T. (2008).  
1488 Beyond existence and aiming outside the laboratory: estimating  
1489 frequency-dependent and pay-off-biased social learning strategies. —  
1490 Philosophical Transactions of the Royal Society B: Biological Sciences 363,  
1491 3515-3528.
- 1492 MCELREATH, R., LUBELL, M., RICHERSON, P., WARING, T., BAUM, W., EDSTEN, E., EFFERSON,  
1493 C. & PACIOTTI, B. (2005). Applying evolutionary models to the laboratory  
1494 study of social learning. — Evolution and Human Behavior 26, 483-508.
- 1495 MERCADER, J., BARTON, H., GILLESPIE, J., HARRIS, J., KUHN, S., TYLER, R. & BOESCH, C.  
1496 (2007). 4,300-Year-old chimpanzee sites and the origins of percussive  
1497 stone technology. — Proceedings of the National Academy of Science 104,  
1498 3043-3048.
- 1499 MESOUDI, A. (2011a). Variable Cultural Acquisition Costs Constrain Cumulative  
1500 Cultural Evolution. — PLoS One 6, e18239.
- 1501 —. (2011b). Variable cultural acquisition costs constrain cumulative cultural  
1502 evolution. — PLoS ONE 6, e18239.
- 1503 MESOUDI, A. & WHITEN, A. (2008). The multiple roles of cultural transmission  
1504 experiments in understanding human cultural evolution. — Philosophical  
1505 Transactions of the Royal Society B: Biological Sciences 363, 3489-3501.
- 1506 MIDFORD, P. E., HAILMAN, J. P. & WOOLFENDEN, G. E. (2000). Social learning of a novel  
1507 foraging patch in families of free-living Florida scrub-jays. — Animal  
1508 Behaviour 59, 1199-1207.
- 1509 MORGAN, T. J. H. & LALAND, K. N. (2012). The biological bases of conformity. —  
1510 Frontiers in neuroscience 6, 87-87.



- 1511 MORGAN, T. J. H., RENDELL, L. E., EHN, M., HOPPITT, W. & LALAND, K. N. (2012). The  
 1512 evolutionary basis of human social learning. — *Proceedings of the Royal*  
 1513 *Society B: Biological Sciences* 279, 653-662.
- 1514 NAHALLAGE, C. A. D. & HUFFMAN, M. A. (2008). Comparison of Stone Handling  
 1515 Behavior in Two Macaque Species: Implications for the Role of Phylogeny  
 1516 and Environment in Primate Cultural Variation. — *American Journal of*  
 1517 *Primatology* 70, 1-9.
- 1518 NIELSEN, M. & TOMASELLI, K. (2010). Overimitation in Kalahari Bushman Children  
 1519 and the Origins of Human Cultural Cognition. — *Psychological Science* 21,  
 1520 729-736.
- 1521 OVERINGTON, S. E., MORAND-FERRON, J., BOOGERT, N. J. & LEFEBVRE, L. (2009).  
 1522 Technical innovations drive the relationship between innovativeness and  
 1523 residual brain size in birds. — *Animal Behaviour* 78, 1001-1010.
- 1524 PANGER, M., PERRY, S., ROSE, L., GROS-LOUIS, J., VOGEL, E., MACKINNON, K. & BAKER, M.  
 1525 (2002). Cross-site differences in foraging behavior of white-faced  
 1526 capuchins (*Cebus capucinus*). — *American Journal of Physical*  
 1527 *Anthropology* 119, 52-66.
- 1528 PERRY, S. (2008). Manipulative monkeys: the capuchins of Lomas Barbudal. —  
 1529 —. (2011). Social traditions and social learning in capuchin monkeys (*Cebus*). —  
 1530 *Royal Society Philosophical Transactions Biological Sciences* 366, 988-  
 1531 996.
- 1532 PERRY, S., BAKER, M., FEDIGAN, L., GROS-LOUIS, J., JACK, K., MACKINNON, K. C., MANSON, J.  
 1533 H., PANGER, M., PYLE, K. & ROSE, L. (2003). Social conventions in wild white-  
 1534 faced capuchin monkeys: Evidence for traditions in a neotropical primate.  
 1535 — *Current Anthropology* 44.
- 1536 PIKE, T. W., KENDAL, J., RENDELL, L. R. & LALAND, K. N. (2010). Learning by  
 1537 proportional imitation in a species of fish. — *Behavioural Ecology* 21,  
 1538 570-575.
- 1539 PINKER, S. & JACKENDOFF, R. (2005). The faculty of language: what's special about  
 1540 it? — *Cognition* 95, 201-236.
- 1541 POWELL, A., SHENNAN, S. J. & THOMAS, M. G. (2009). Late Pleistocene demography  
 1542 and the appearance of modern human behavior. — *Science* 324, 1298-  
 1543 1301.
- 1544 —. (2010). Demography and Variation in the Accumulation of Culturally  
 1545 Inherited Skills. — In: *Innovation in Cultural Systems. Contributions from*  
 1546 *Evolutionary Anthropology* (M. J. O'Brien & S. J. Shennan, eds). MIT Press,  
 1547 London, p. 137-160.
- 1548 PRADHAN, G. R., TENNIE, C. & VAN SCHAIK, C. P. (2012). Social organization and the  
 1549 evolution of cumulative technology in apes and hominins. — *Journal of*  
 1550 *Human Evolution* 63, 180-190.
- 1551 PREMACK, D. (2007). Human and animal cognition: Continuity and discontinuity.  
 1552 — *Proceedings of the National Academy of Sciences* 104, 13861.
- 1553 PRICE, E. E., LAMBETH, S. P., SCHAPIRO, S. J. & WHITEN, A. (2009). A potent effect of  
 1554 observational learning on chimpanzee tool construction. — *Proceedings*  
 1555 *of the Royal Society B: Biological Sciences* 276, 3377-3383.
- 1556 RAIHANI, N. J. & RIDLEY, A. R. (2008). Experimental evidence for teaching in wild  
 1557 pied babblers. — *Animal Behaviour* 75, 3-11.
- 1558 READER, S. & LALAND, K. (2001). Primate innovation: sex, age and social rank  
 1559 differences. — *International Journal of Primatology* 22, 787-805.

- 1560 —. (2002). Social intelligence, innovation, and enhanced brain size in primates.  
1561 — Proceedings of the National Academy of Sciences 99, 4436.
- 1562 READER, S. M. & BIRO, D. (2010). Experimental identification of social learning in  
1563 wild animals. — Learning and Behavior 38, 265-283.
- 1564 RENDELL, L., BOYD, R., COWNDEN, D., ENQUIST, M., ERIKSSON, K., FELDMAN, M. W.,  
1565 FOGARTY, L., GHIRLANDA, S., LILICRAP, T. & LALAND, K. N. (2010). Why copy  
1566 others? Insights from the social learning tournament. — Science 328, 208-  
1567 213.
- 1568 RICHERSON, P. & BOYD, R. (2005). Not by Genes Alone: How culture transformed  
1569 human evolution. — University of Chicago Press, Chicago.
- 1570 SANZ, C. & MORGAN, D. (2007). Chimpanzee tool technology in the Goulougo  
1571 Triangle, Republic of Congo. — Journal of Human Evolution 52, 420-433.
- 1572 —. (2009). Flexible and Persistent Tool-using Strategies in Honey-gathering by  
1573 Wild Chimpanzees. — International Journal of Primatology 30, 411-427.
- 1574 SANZ, C. M., SCHONING, C. & MORGAN, D. B. (2009). Chimpanzees Prey on Army Ants  
1575 with Specialized Tool Set. — American Journal of Primatology 71, 1-8.
- 1576 SCHLAG, K. H. (1998). Why Imitate, and If So, How?: A Bounded Rational Approach  
1577 to Multi Armed Bandits. — Journal of Economic Theory 78, 130-156.
- 1578 SEED, A., CLAYTON, N. & EMERY, N. (2007). Postconflict third-party affiliation in  
1579 rooks, *Corvus frugilegus*. — Current Biology 17, 152-158.
- 1580 SOMA, M. & HASEGAWA, T. (2004). The effect of social facilitation and social  
1581 dominance on foraging success of budgerigars in an unfamiliar  
1582 environment. — Behaviour 141, 1121-1134.
- 1583 STERELNY, K. (2009). Peacekeeping in the Culture Wars. — In: The Question of  
1584 Animal Culture (K. N. Laland & B. G. Galef, eds). Harvard University Press,  
1585 Cambridge.
- 1586 SUGIYAMA, Y. (1997). Social tradition and the use of tool-composites by wild  
1587 chimpanzees. — Evolutionary Anthropology 6, 23-27.
- 1588 TENNIE, C., CALL, J. & TOMASELLO, M. (2009). Ratcheting Up the Ratchet: On the  
1589 Evolution of Cumulative Culture. — Philosophical Transactions of the  
1590 Royal Society Series B 364, 2405.
- 1591 —. (2012). Untrained Chimpanzees (*Pan troglodytes*  
1592 *schweinfurthii*) Fail to Imitate Novel Actions. — PLoS ONE 7,  
1593 e41548.
- 1594 THIERRY, B., AURELI, F., NUNN, C. L., PETIT, O., ABEGG, C. & DE WAAL, F. B. M. (2008). A  
1595 comparative study of conflict resolution in macaques: insights into the  
1596 nature of trait covariaion. — Animal Behaviour 75, 847-860.
- 1597 THORNTON, A. & MCAULIFFE, K. (2006). Teaching in wild meerkats. — Science 313,  
1598 227-229.
- 1599 TOMASELLO, M. (1994). The question of chimpanzee culture. — In: Chimpanzee  
1600 Cultures (R. W. Wrangham, W. C. McGrew, F. B. M. de Waal & P. G. Heltne,  
1601 eds). Harvard University Press, Cambridge, MA, p. 301-377.
- 1602 —. (1999). The Cultural Origins of Human Cognition. — Harvard University  
1603 Press, London.
- 1604 TOMASELLO, M. & CALL, J. (1997). Primate Cognition. — Oxford University Press,  
1605 Oxford.
- 1606 TOMASELLO, M. & CARPENTER, M. (2007). Shared Intentionality. — Developmental  
1607 Science 10, 121-125.

- 1608 TOMASELLO, M., CARPENTER, M., CALL, J., BEHNE, T. & MOLL, H. (2005). Understanding  
1609 and sharing intentions: The origins of cultural cognition. — *Behavioral*  
1610 *and Brain Sciences* 28, 675-735.
- 1611 TOMASELLO, M., KRUGER, A. C. & RATNER, H. H. (1993). Cultural Learning. —  
1612 *Behavioral and Brain Sciences* 16, 495-552.
- 1613 TOMASELLO, M. & MOLL, H. (2010). The Gap is Social: Human Shared Intentionality  
1614 and Culture. — In: *Mind the Gap. Tracing the Origins of Human Universals*  
1615 (P. M. Kappeler & J. B. Silk, eds). Springer, Berlin.
- 1616 VAN DER POST, D. & HOGEWEG, P. (2008). Diet traditions and cumulative cultural  
1617 processes as side-effects of grouping. — *Animal Behaviour* 75, 133-144.
- 1618 VAN SCHAIK, C. P., ANCRENAZ, M., BORGES, G., GALDIKAS, B., KNOTT, C. D., SINGLETON, I.,  
1619 SUZUKI, A., UTAMI, S. S. & MERRILL, M. (2003). Orangutan cultures and the  
1620 evolution of material culture. — *Science* 299, 102-105.
- 1621 WARNER, R. R. (1988). Traditionality of mating-site preferences in a coral reef fish.  
1622 — *Nature* 335, 719-721.
- 1623 WHITEN, A., CUSTANCE, D., GOMEZ, J., TEIXIDOR, P. & BARD, K. (1996). Imitative  
1624 learning of artificial fruit processing in children (*Homo sapiens*) and  
1625 chimpanzees (*Pan troglodytes*). — *Journal of Comparative Psychology*  
1626 110, 3-14.
- 1627 WHITEN, A., GOODALL, J., MCGREW, W. C., NISHIDA, T., REYNOLDS, V., SUGIYAMA, Y., TUTIN,  
1628 C. E. G., WRANGHAM, R. W. & BOESCH, C. (1999). Cultures in chimpanzees. —  
1629 *Nature* 399, 682-685.
- 1630 WHITEN, A., HORNER, V. & DE WAAL, F. (2005). Conformity to cultural norms of tool  
1631 use in chimpanzees. — *Nature* 437, 737-740.
- 1632 WHITEN, A., MCGUIGAN, N., MARSHALL-PESCINI, S. & HOPPER, L. (2009). Emulation,  
1633 Imitation, Overimitation and the Scope of Culture for Child and  
1634 Chimpanzee — *Philosophical Transactions of the Royal Society B:*  
1635 *Biological Sciences* 364, 2417-2428.
- 1636 WHITEN, A. & VAN SCHAIK, C. (2007). The evolution of animal ‘cultures’ and social  
1637 intelligence. — *Philosophical Transactions of the Royal Society B:*  
1638 *Biological Sciences* 362, 603-620.
- 1639 WISDOM, T. N. & GOLDSTONE, R. L. (2010). Social learning and cumulative mutual  
1640 improvement in a networked group. — In: *Proceedings of the 32nd*  
1641 *Annual Conference of the Cognitive Science Society* (S. Ohlsson & R.  
1642 Catrambone, eds), Austin, TX, p. 1405-1410.
- 1643 WOOD, L., KENDAL, R. L. & FLYNN, E. (2012). Context dependent model-based biases  
1644 in cultural transmission: Children's imitation is affected by model age  
1645 over model knowledge state. — *Evolution and Human Behavior* 104, 367-  
1646 381.
- 1647 WOOD, L.A., KENDAL, R.L. & FLYNN, E.G. (2013) Copy me or copy you? The effect of  
1648 prior experience on social learning. *Cognition*, 127: 203-213
- 1649 ZIMAN, J. (2000). *Real Science: What it is and what it means.* — Cambridge  
1650 University Press, Cambridge.
- 1651
- 1652