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HUMAN CUMULATIVE CULTURE: A COMPARATIVE PERSPECTIVE

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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 20th 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 20th 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

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 18th
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

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1222

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