

1 Culture Extends the Scope of Evolutionary Biology in the Great Apes  
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16 Discoveries about the cultures and cultural capacities of the great apes have played a  
17 leading role in the recognition emerging in recent decades that cultural inheritance can  
18 be a significant factor in the lives not only of humans, but of non-human animals. This  
19 prominence derives in part from the fact that these primates are those with whom we  
20 share the most recent common ancestry, thus offering clues to the origins of our own  
21 thoroughgoing reliance on cumulative cultural achievements. In addition, the intense  
22 research focus on these species has spawned an unprecedented diversity of  
23 complementary methodological approaches, the results of which suggest that cultural  
24 phenomena pervade the lives of these apes, with potentially major implications for their  
25 broader evolutionary biology. Here I review what this extremely broad array of  
26 observational and experimental methodologies has taught us about the cultural lives of  
27 chimpanzees, gorillas and orangutans, and consider the ways in which this extends our  
28 wider understanding of primate biology and the processes of adaptation and evolution  
29 that shape it. I address these issues by first evaluating the extent to which the results of  
30 cultural inheritance echo a suite of core principles that underlie organic, Darwinian  
31 evolution, but also extend them in new ways; and secondly by assessing the principal  
32 causal interactions between the primary, genetically-based organic processes of  
33 evolution, and the secondary system of cultural inheritance that is based on social  
34 learning from others.

35

36 Social learning | culture | evolutionary biology | chimpanzee | gorilla | orangutan

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40 Recent decades have revealed social learning (learning from others) to be pervasive  
41 across the animal kingdom, with important implications for evolutionary biology at  
42 large (1), the subject of the Sackler Colloquium published here (2). The present article  
43 focuses on great apes: chimpanzee (*Pan troglodytes*), gorilla (*Gorilla gorilla*) and  
44 orangutan (*Pongo pygmaeus*). Other primates are dealt with elsewhere in the issue (3,  
45 4). Despite an early report (5) we still know little about cultural phenomena in  
46 chimpanzees' rarer sister species, the bonobo (*Pan paniscus*) so bonobos are omitted  
47 here. I also make only limited reference to human culture, despite the fact we are  
48 technically also 'great apes'. Human culture is extensively treated in other papers in the  
49 issue.

50 I first survey the nature and scope of social learning and associated aspects of  
51 cultural transmission in great apes, concluding that the depth and diversity of  
52 observational and experimental evidence for cultural phenomena is unparalleled  
53 amongst non-human species. The evidence thus accumulated suggests that culture  
54 permeates the lives of the great apes in the breadth of behavioral repertoires affected,  
55 and also in their time-depth. This makes them evolutionarily significant. The authors of  
56 a comprehensive recent review of cetacean culture concluded that "Culture ... is a  
57 major part of what the whales are" (6, p. 7; and see 7). Such a statement is obviously  
58 true for our own species (8-11); here I examine the justifications for thinking the phrase  
59 also has validity for great apes.

60 Following a sister review ranging much more widely across both vertebrates and  
61 invertebrates (1), I take eight core principles of evolution illuminated by Darwin (12)  
62 and assess the extent to which they apply to cultural phenomena in the great apes  
63 (henceforth simply 'apes'), as they do in humans (13). I then explore ways in which  
64 cultural inheritance goes yet further beyond these principles, creating new evolutionary  
65 phenomena. Finally I address interactions between the primary manifestations of  
66 organic evolution based on genetic inheritance, and the 'second inheritance system' (14)  
67 based on social learning. In a now long-standing human literature this has been called  
68 'gene-culture co-evolution' (15), the logic of which (10, 16) should apply to other  
69 cultural animals (1, 7).

70

71 **Diverse and Convergent Evidence for the Scope of Great Ape Culture**

72

73 **Geographic variation in traditions in the wild.** In 1986 Goodall began to chart  
74 differences behavior patterns between chimpanzee study sites across Africa (17),  
75 proposing these as cultural variants where no genetic or environmental explanation was  
76 apparent (later called the ‘method of exclusion’). The approach became more  
77 comprehensive with time (18, 19), eventually benefitting from a systematic  
78 collaboration between multiple long-term research groups (20, 21). The same was soon  
79 achieved by orangutan field researchers (22) and more recently by a gorilla consortium  
80 (23). These analyses converged in reporting multiple cultural variants in all three  
81 genera: 39 (*Pan*); 24 (*Pongo*) and 23 (*Gorilla*). These spanned apes’ behavioral  
82 repertoires, including a great variety of tool use, food processing and social behavior,  
83 discussed further below. Further variants have continued to be intermittently reported  
84 for *Pan* (24) and *Pongo*, in the latter case leading to a revised tally of between 26-35  
85 variants depending upon the criteria applied (25).

86 These surveys are vulnerable to false positives (it can be difficult to be sure that all  
87 alternatives to social learning have been excluded), and also false negatives (cultural  
88 adaptations to local environmental properties may be inappropriately excluded) (26).  
89 However, these pioneering efforts provided essential platforms for more refined  
90 approaches, some incorporating both genetic and environmental variables into analyses  
91 (27). Other advances yielded confirmatory evidence for culture through (i) more  
92 focused micro-habitat analyses for specific behaviors such as ant-dipping (28, 29); (ii)  
93 comparisons between neighboring communities sharing genes and habitat properties  
94 (30); and (iii) social learning experiments, as for nut-cracking (31-32)..

95 The broad geographic surveys thus provide an initially imperfect but progressively  
96 refined overall picture of ape cultural repertoires. The approach has been systematically  
97 applied to spider monkeys (*Ateles*, reporting 23 cultural variants) (33) but to my  
98 knowledge, not yet to other animals. Evidence exists for multiple cultural variants in  
99 other species such as killer whales, that display very different hunting repertoires (e.g.  
100 for fish versus seals), song repertoires and migratory patterns (6), but systematic  
101 tabulations have yet to facilitate direct cross-species comparisons.

102

103 **Inter-group variation in traditions in captive communities.** A parallel approach has  
104 compared neighboring communities in captive contexts, with the advantage that genetic  
105 and environmental explanations for group differences can be dismissed more cleanly.  
106 For example in the Chimpfunshi chimpanzee sanctuary in Zambia, a bizarre habit of  
107 inserting a blade of grass into one ear and leaving it there spread in one group but not in  
108 others (34). Moreover a distinctive ‘hand-clasp’ form of grooming was absent in this  
109 group and one other, yet customary in others where it additionally took different forms  
110 (35). Similar group contrasts were found in hard-shelled Strychnos fruits were opened  
111 (36), whilst at the Yerkes Center in the USA a further contrast in hand-clasp grooming  
112 emerged and spread over several years, remaining absent in another (37). These results  
113 reinforce those derived from the studies in the wild, outlined above.

114

115 **Quantitative Evidence for Vertical, Mother to Offspring Transmission.** A study of  
116 the ontogeny of using stem-tools for termite-fishing found that juvenile female  
117 chimpanzees spent significantly more time attending to their mother’s fishing than did  
118 their male peers (38). Consistent with the skill being learned by observation, the young  
119 females tended to master the technique a whole year ahead of the males, with a  
120 significant tendency to match even the length of probe their mother typically inserted  
121 into the mound (38).

122 Researchers studying orangutans have called the focused visual attention of  
123 juveniles ‘peering’ (39) (see Fig.1). Building on studies documenting correlations  
124 between maternal and juvenile foraging profiles (40, 41), a suite of predictions were  
125 confirmed consistent with peering functioning to facilitate learning key survival skills  
126 (39). In foraging and nest-building contexts where peering is most frequent, it was  
127 found that (i) the frequency of peering in foraging contexts was predicted by the  
128 quantified complexity of processing operations and also by the skill’s rarity; (ii) peering  
129 was followed by a higher rate of exploration of the item concerned, also confirmed  
130 specifically for the use of sticks in foraging, seen only at one of the two sites studied;  
131 (iii) peering rose along with the learning of new skills and diminished as competence  
132 was achieved; (iv) peering at nest-building was followed by a rise in nest-building over  
133 the next hour; (iv) developmentally, peering tracked the peak time of learning to make  
134 nests; and (v) by about age five, peering tipped below 50% directed at a juvenile’s

135 mother and more towards others, from whom there was yet something to learn (39).  
136 Such observations offer a compelling case that juvenile apes' close peering facilitates  
137 learning major life skills.

138

139 < insert Fig. 1 about here >

140

141 **Quantitative Evidence for Horizontal Transmission.** There is both intra-community  
142 and inter-community evidence for horizontal transmission in the wild. An example of  
143 the former was tracked by network-based diffusion analysis, confirming that a novel  
144 chimpanzee behavior, using moss as water-sponge, spread from the alpha male along  
145 lines of social affiliation, providing quantitative circumstantial evidence for  
146 transmission (42). Examples of inter-community transmission include (i) a significant  
147 acceleration in habituation to human observers in a chimpanzee community being newly  
148 habituated, after two females immigrated from a well habituated community (43); and  
149 (ii) ant-fishing spread to a new community after the immigration of a proficient  
150 individual from a neighboring community where fishing was habitual (44).

151

152 **Quantitative and Qualitative Evidence for Investment in Transmission.** Video of  
153 termite fishing has documented skilled chimpanzee mothers donating tools to less  
154 competent juveniles (Supplementary Fig. S1), thence suffering a diminished duration  
155 and rate of termiting, whereas the recipient enjoyed improved fishing (45). The authors  
156 propose this meets commonly accepted criteria for a functional (as opposed to  
157 intentional) concept of 'teaching'. They also document mothers orally splitting their  
158 tool lengthwise to neatly make two functional tools, or bringing multiple tools,  
159 suggesting this partially buffers mothers from the costs of youngsters' demands.  
160 Alternatively it might be argued that these actions are essentially unnecessary and so  
161 represents the more compelling evidence the behavior has costs and therefore counts as  
162 teaching, even if not as active as teaching by scorpion provision in meerkats (46) or  
163 beaching to catch seals in killer whales (6). However, the pattern of costs and benefits  
164 suggests that this support has positive fitness benefits to the young, and parallel reports  
165 concerning use of tools for nutcracking have also been described (47).

166 An earlier report described more active involvement in curbing youngsters'  
167 exploration of potentially dangerous food-types. Haraiwa-Hasegawa (48, p. 280)  
168 reported that when an infant PN reached to touch some fig leaves, "her mother, FT, took  
169 PN's hand and moved it away from the leaves. As PN continued ... FT took the leaves  
170 from PN's hand, plucked all the leaves within her arm's reach and dropped them to the  
171 ground." At least one other mother behaved similarly and "prohibited their infants only  
172 from feeding on the individual trees that they themselves never fed on".

173

174 **Dyadic Experimental Studies of Social Learning.** Experimental reports of social  
175 learning by naïve individuals from proficient models have multiplied for over a century  
176 in all great ape genera, tabulated and enumerated in successive reviews (49: n = 19  
177 studies; 50: n = 33 further studies; 51: n = 25 studies comparing two or more ape  
178 species). The more recent experiments often adopt a highly informative 'two-action'  
179 approach, in which participants see either of two models, each trained to tackle a  
180 problem like opening a foraging box in a different way. Ideally a third, no-model  
181 control group is included. This method has demonstrated social learning in captive  
182 chimpanzees (52), gorillas (53) and orangutans (54), that implies the copying of  
183 whichever of the two actions (imitation) or movements of the manipulanda (emulation)  
184 were seen, rather than simpler processes of mere enhancement of the manipulanda (55).  
185 These approaches have further dissected the particular social learning processes at work,  
186 a topic beyond the scope of this review (see 56-59 for in-depth treatment). More  
187 relevant to present concerns and reviewed further below are extensions to these  
188 approaches to track successive cultural transmissions necessary to sustain traditions.

189 Nevertheless these dyadic experiments can importantly complement results from  
190 the field. For example, nut-cracking with natural hammer materials, found naturally  
191 only in West Africa (Fig. 2) is shown not explicable as an instinct in the West that is  
192 simply absent in the East, for East African chimpanzees exposed to proficient models  
193 became proficient, unlike controls in a no-model control condition, showing the  
194 behavior is (socially) learned (31, 32) (Fig. 2).

195

196 < insert Fig. 2 about here >

197

198 **Cultural Diffusion Experiments.** Experiments focused on the broader phenomenon of  
199 cultural diffusion typically begin with models displaying different solutions to a task  
200 and then track their potential spread in others who witness them. Alternative variants  
201 provide important complementary information (63, 64). For example, the ‘transmission  
202 chain’ design pairs a first model (A) with a naïve individual (B), then when B achieves  
203 some competence criterion, they become a model for a further individual, and so on (B-  
204 C, C-D etc.). Achieving such configurations peacefully with apes requires sensitive  
205 experimental manouevering, but transmission has been demonstrated along chains of up  
206 to five participants in chimpanzees (65) and orangutans (66), as in children (65). This  
207 provides important models of transmission across cultural ‘generations’, implying a  
208 potential for cultural transmission across what would naturally be decades of ape life.

209 By contrast, ‘open diffusion’ designs mimic transmission in the wild where whole  
210 groups are exposed to alternative models; it is ‘open’ who watches and copies (or not).  
211 This design has been applied in chimpanzees and children in several experiments (67-  
212 69), including two where tool-use behavioral variants were transmitted across three  
213 groups with significant fidelity (69). This is important for interpreting putative cultures  
214 in the wild, such as the nut-cracking distributed across several hundred kilometers of  
215 West Africa, that would have required repeated inter-community transmission.

216

## 217 **How Pervasive is the Role of Cultural Inheritance in the Lives of Great Apes?**

218

219 **Social Learning Shapes a Broad Repertoire of Cultural Variants.** We can first  
220 examine this question by surveying the range of behaviors described in the cross-site  
221 comparisons summarized above (20-23, 27).

222 The chimpanzee lists of 1999-2001 include 30 different kinds of tool use ascribed  
223 to culture, all suggesting functional and adaptive payoffs beneficial to the performer’s  
224 biological fitness (14, 21, 24). Others have been reported since, including sticks bitten  
225 and thus sometimes made sharp, used to stab or evict bushbaby prey at Fongoli in  
226 Senegal (70, 71) and a kit of stout tools to make tunnels, plus fine stems to fish down  
227 these and extract termites from nests deep underground (72). A majority of such tools  
228 are used in food extraction, but others are used in ‘hygienic’ actions like wiping blood  
229 or semen off fur, in protective ‘comfort’ roles such as leaf-cushions on wet ground, and



230 in local courtship gambits such as bending small shrubs on the ground (20, 21). Other  
231 diverse items include forms of food processing without tools, ways of dispatching ecto-  
232 parasites located during grooming, and grooming customs like the ‘hand-clasp’ that  
233 shows variant forms even in neighboring communities (73).

234 The orangutan list of 2003 (22) also includes a dozen different forms of tool use,  
235 several used for food extraction, such as holding a small stick in the mouth to extract  
236 seeds from *Neesia* fruits, or ‘leaf-gloves’ to handle spiky fruit. Hygiene/comfort  
237 examples include using a leaf napkin to wipe off sticky latex. The list as a whole is  
238 diverse, incorporating forms of arboreal locomotion, vocal sounds (some modified  
239 using leaves), variant nest constructions such as adding sun covers, and whether slow  
240 lorises are eaten or not, irrespective of availability.

241 The recent gorilla list of putative cultural variants (23) also displays diversity that  
242 includes making bridges across water, rubbing fruit to clean it or remove spines,  
243 incorporating tree-slapping into displays, using teeth as a ‘fifth limb’ in climbing, forms  
244 of bodily contact while travelling together, and forms of social play.

245

246 **The Extent of Vertical Inter-generational Transmission.** A detailed study of the  
247 foraging behavior of young wild orangutans before and after weaning concluded that  
248 their “diets were essentially identical to their mothers’ even though not all mothers had  
249 the same diet” ... “immatures selectively observed their mothers during extractive  
250 foraging, which increased goal-directed practice but not general manipulation of similar  
251 objects, suggesting observational forms of learning of complex skills” (40, p. 62). This  
252 conclusion was reinforced by a later study focused on ‘peering’ (39), referred to earlier.  
253 Over 2-4 years of age, infants foraged with their mother over 90% of the time; 94% of  
254 their feeding time was when the mother was also feeding, and 96% of their feeding was  
255 on the same items (39). The extent of co-feeding is clearly massive in pre-weaning  
256 years and likely to engender vertical social transmission of dietary profiles.

257 Years of mother-offspring association and co-feeding are typical of all the great  
258 apes and appears to lay down dietary preferences that change relatively little after  
259 weaning. Although the social learning implied may be as simple as enhancement of a  
260 food type by the mother feeding on it, such effects are likely to be profoundly important  
261 because large diet-sets need to be mastered, and selected from the yet more vast options

262 a tropical forest offers. This includes avoiding the numerous plant parts that are toxic,  
263 selecting relatively nutritious options and avoiding relatively poor ones. Chimpanzees  
264 may eat over 300 different food types (species x parts) in a year (74), and in the Lopé  
265 Park of Gabon, for example, fruit alone is taken from 114 different plants (75), selected  
266 from among many hundreds of potential food types available. The diet of gorillas may  
267 be similarly diverse, with gorillas in the Alfi mountains of Cameroon eating over 200  
268 different food types, including fruits, seeds, leaves, stems, pith, flowers, bark, roots and  
269 invertebrates (75); and for the orangutans of Tanjung Puting in Borneo, the figure is  
270 again over 300 different food types (76). Yet the dietary profile of different populations  
271 may vary much, as suggested by earlier chimpanzee studies (77) and more recently  
272 confirmed even for neighbouring orangutan populations separated by a large river, that  
273 displayed 60% difference in diet, contrasting with intra-population homogeneity (78).  
274 Years of close apprenticeship to a mother who daily displays her knowledge of such a  
275 large yet selective diet-set likely offers an important means of achieving an adaptive  
276 response to this challenging complexity.

277

278 **Time Depth of Cultural Transmission.** Long-term field sites have shown that  
279 techniques such as termite fishing continue across several generations during the half-  
280 century of research now achieved. However this pales in comparison to the discoveries  
281 of real archaeological excavation, which in the Tai Forest of Ivory Coast reached a  
282 depth corresponding to 4,300 years, where remains of nut-cracking were identified  
283 (illustrated in figure 1 of reference (1)) beneath those currently generated on the surface  
284 by chimpanzees (79). Of course, this behavior may be very much older. Once such a  
285 beneficial technology becomes customary, it may continue in perpetuity pending major  
286 ecological perturbation. This example suggests that ape cultural inheritance spans not  
287 only the breadth of behavioral repertoires outlined earlier, but also a potentially  
288 significant time depth comparable to that familiar in organic evolution via genetic  
289 inheritance.

290

291 **Does Ape Culture Instantiate A ‘New’ Form of Evolution?**

292

293 Ape culture may have pervasive effects in shaping the behavioral repertoires of  
294 successive generations in the ways reviewed above, but does this imply an ‘extension of  
295 biology’ in the sense of instantiating a new form of evolution based not on genetic, but  
296 on social inheritance? This is what Dawkins proposed in his concept of culturally  
297 replicated ‘memes’ as analogies of genes, creating a new form of evolution in the case  
298 of human culture (80). The idea of aspects of culture such as language evolving through  
299 variation, (cultural) inheritance and selection goes back to Darwin’s own writings (81)  
300 and was highlighted as the tenth and latest ‘major evolutionary transition’ of those  
301 proposed by Maynard-Smith and Szathmary (82). Mesoudi et al. (13) tackled the issue  
302 in finding abundant evidence for counterparts in human culture of eight major principles  
303 Darwin set out in the *Origin* (12): variation, selection, inheritance, adaptation,  
304 accumulation of modifications, geographic variation, convergence and changes of  
305 function. How do apes compare?

306 In addressing this we must be clear about what phenomena we are querying the  
307 potential ‘evolution’ of. If a chimpanzee invents a better hammer for nut-cracking  
308 (perhaps using a stone rather than wood), this may enhance that individual’s biological  
309 fitness, with its genes better represented in future generations. That is natural selection,  
310 shaping biological evolution. However if others *copy* use of the new tool, the fitness  
311 (reproductive success) of that *cultural entity* – stone-tool use – will be enhanced through  
312 its spread, and to this extent we have *cultural evolution* of this *behavior*. It is this  
313 second phenomenon we are addressing here. Effects on individual culture-bearer’s  
314 biological, inclusive fitness are a different matter and are returned to in a later section  
315 further below. We can now consider the eight evolutionary principles noted above.

316  
317 **Variation, Selection and Inheritance.** These three principles can together be regarded  
318 as the core ‘trinity’ of Darwinian evolution. Their joint working is an ‘evolutionary  
319 algorithm’ that has been suggested to have the power to explain a multitude of  
320 phenomena beyond the living systems Darwin showed it applied to (83, 84).

321 As we have seen above, there is plentiful evidence in the great apes for the feature  
322 of *inheritance*, through social learning that provides sufficient fidelity to sustain  
323 traditions. There is also cultural *variation*, in part because compared to gene replication,  
324 social learning is prone to imperfect copying. In the arrays of cultural variants among

325 great apes discussed earlier in this article, there are plenty of behaviors that are  
326 displayed by many individuals in a community but not all (classed as ‘habitual’, rather  
327 than ‘customary’).

328 By contrast there seems yet to be little direct recording of cultural evolutionary  
329 *change* through *competition* and *selection* within this variation. This is perhaps  
330 unsurprising. During the human Stone Age, even when sophisticated, bilaterally-  
331 symmetric Acheulian blades showed an advance over earlier crude Oldowan tools, they  
332 changed relatively little over a million years (85). If such stability not implausibly  
333 characterizes chimpanzee nut-cracking and other cultural variants of apes, then we will  
334 see little evidence of cultural selection in human lifetimes. Of course, organic  
335 evolutionary change is itself often slow compared to scientific lifetimes; and instructive  
336 exceptions have often followed human-caused environmental perturbations that create  
337 new selection pressures. The classic example is of selection favoring dark morphs of  
338 peppered moths, better camouflaged against the sooty surfaces of the industrial  
339 revolution, then flipping to favor light colored morphs as the world became cleaner  
340 again.

341 Accordingly I have suggested that similar contexts of anthropogenic change may be  
342 fruitful for investigating cultural evolution in animals (1). Scientific experiments may  
343 offer a convenient instance. For example, in a pioneering cultural diffusion study, three  
344 juvenile chimpanzees were confronted with and avoided two novel objects (86). One  
345 youngster was then replaced with a naïve one, and this repeated, so after every third  
346 such cycle the triplet contained different individuals than earlier. Nevertheless,  
347 approaches to the objects steadily increased and in later ‘generations’ became  
348 customary (Supplementary Fig. S2). Accordingly, here there was *variation* in boldness,  
349 *inheritance* by naïve youngsters learning from bolder ones that the objects could be  
350 safely approached and explored, and competitive *selection* favoring small progressive  
351 steps in boldness. Playing with the objects could thus evolve as the norm in later  
352 generations, composed of different youngsters than the original shy ones. In a  
353 counterpart from the wild, two individuals from a human-habituated community of wild  
354 chimpanzees immigrated into a neighboring community that scientists were beginning  
355 to habituate, at which point habituation accelerated significantly (43).

356 In these examples an initially common variant (caution) was replaced competitively  
357 by another (boldness) which was adaptively superior (fear was unnecessary in these  
358 contexts). Likewise, in all the cultural diffusion experiments with apes cited earlier,  
359 improved foraging techniques spread across test groups to replace the less competitive  
360 behavioral state characterized by their absence. Here again there was thus *variation*  
361 (although in this case, experimenter-engineered), *inheritance* via social learning, and  
362 *competitive selection* favoring the cultural spread of the new foraging technique.

363 I suggest such experiments (as in 86) may thus allow us to explore the capacity of  
364 apes to exemplify, even if in a limited way, the operation of the ‘Darwinian trinity’  
365 algorithm in a cultural context. Presumably all the cases of clearly beneficial cultural  
366 variants in the wild, like nut-cracking and other tool use, once did not exist; so where  
367 they are customary this is likely to have arisen through the operation of this algorithm.

368

369 **Adaptation.** The growth of boldness in the studies above (43, 86) indicate culturally  
370 evolved instances of *adaptation*, although adaptive payoffs were likely only mild. In the  
371 wild there is evidence that a more crucial level of adaptiveness has been delivered.  
372 Chimpanzees in Bossou, Guinea, were shown to be reliant on two forms of technology  
373 in particular, nut-cracking and pestle-pounding (a means of extracting nutritious pulp  
374 from the apex of palm trees), during the dry season when fruit became scarce (87), such  
375 that it is these cultural variants that allow these apes to inhabit otherwise inadequate  
376 habitats. How often culturally inherited technology is this critical remains difficult to  
377 judge at present, but many forms of tool use allow chimpanzees and orangutans to gain  
378 foodstuffs otherwise unavailable.

379 Such adaptations concern the local physical environment. Others may be societal.  
380 In a community of chimpanzees that customarily practice hand-clasp grooming, it may  
381 be adaptive to learn this from those already using it; and where a particular courtship  
382 gambit such as leaf-clipping has become common, it will likely be beneficial to adopt  
383 this as an action already recognized by one’s potential mating partner.

384

385 **Accumulation of Modifications.** Human cultural modifications accumulate in an  
386 elaborate fashion that has no match in other animals, and display the most striking  
387 analogies with the richness of the evolved forms of the living world (9, 10, 13, 16, 83,

388 84). Many authors assert that we are the only species to exhibit cumulative culture (8, 9,  
389 49, 56), but I suggest this may be premature. For example, chimpanzees in Goulougo  
390 use a stout stick to make a deep tunnel to subterranean termite nests and then use long  
391 stems to fish down the tunnels, first creating a distinct brush tip effective for fishing by  
392 stripping the stem ends through their teeth (72). They do this in a context where what to  
393 do is highly opaque, so it is difficult to see how it could have developed other than by a  
394 series of cumulative steps beginning with the more transparent context of fishing near  
395 the surface. Boesch (47) describes several other candidates for cumulative cultural  
396 evolution in chimpanzees. Direct evidence on the origins of such routines are lost in the  
397 past, but their complexity suggests elementary forms of cumulative culture, comparable  
398 perhaps to the achingly slow forms that characterized the early hominin Stone Age.

399

400 **Geographic Variation.** As the Darwinian algorithm operates in different regions, so  
401 organic characteristics differentiate and speciation may occur. Parallel effects occur in  
402 human cultural evolution (13, 88). As we have seen, great apes show evidence of  
403 different traditions at geographically-separated locations, and there is evidence from all  
404 the great ape genera that differences in putative cultural profiles are correlated with the  
405 geographic separation of communities (23, 24). As humans or other apes disperse over  
406 greater distances, one would expect both genetic and cultural similarities to diminish,  
407 and indeed Langergraber et al. (89) showed that cultural variation in chimpanzees is  
408 also correlated with genetic variation (but this does not mean genes explain the  
409 behavioural differences: see supplementary information to ref. 79 for further discussion  
410 of this study). Kamilar and Atkinson (90) demonstrated a nested structure in four  
411 samples of human cultural repertoires in N. America and New Guinea, which would  
412 occur if, as people disperse, traits are sequentially added in or lost. Consistent with  
413 earlier cladistic analyses of the branching pattern of chimpanzee profiles (91),  
414 chimpanzees were also found to display this pattern of nestedness across African sites.  
415 Orangutans did not, consistent with an earlier detailed orangutan study (27) and  
416 possibly reflecting a greater preponderance of vertical, mother-to-offspring transmission  
417 than horizontal transmission between communities.

418

419 **Convergent Evolution.** The Darwinian algorithm delivers some similar organic  
420 evolutionary outcomes in different places, despite different foundations. Cultural  
421 convergences of this kind appear to occur at different layers of relatedness amongst  
422 apes. An example within the same species is hand-clasp grooming, which has emerged  
423 and spread in some chimpanzee communities in the wild, but not others (20, 21, 73) as  
424 well as in an African sanctuary (35) and in groups in the USA (37). This is not simply  
425 individual invention because within-group spread of the behavior has been documented,  
426 indicating social transmission. Other convergences span different ape genera, such as  
427 use of fly swats and leaf napkins by both chimpanzees and orangutans; and again these  
428 are neither species instincts nor individually learned, because they are habitual at some  
429 locations yet absent at others, in the same species. Finally there are convergences  
430 between apes and other primates, as in the case of using stones as hammers to break  
431 open hard-cased food by distantly related long-tailed macaques (92) and capuchins (3,  
432 93).

433  
434 **Change of Function.** This is perhaps the category where we are most limited by lack of  
435 historical records. In humans, historical records suggest that just as morphology can  
436 evolve to serve a new function (arms becoming wings, for example), cultural elements  
437 may evolve new functions different to their original one (10). A candidate in great apes  
438 is that in chimpanzees, ‘leaf-clip’ (noisily shredding leaves with one’s teeth) is reported  
439 as a courtship bid in some communities but used for other functions such as play in  
440 others (47) suggesting some of these alternatives may have evolved from each other or  
441 from a common ancestral function. However, it may yet be that the lack of evidence in  
442 this category is explained by that concerning limited cultural cumulation, noted above.

#### 443 444 **Culture extends Biology into New Realms of Evolution**

445  
446 The above focuses on how cultural evolution may match the ‘template’ for genetically-  
447 based Darwinian evolution, but cultural transmission by social learning also extends the  
448 scope of biological systems by incorporating additional dimensions of inheritance and  
449 evolution. Some of these have long been recognized in the literature concerning human  
450 cultural evolution, including the fact that in addition to intergenerational transmission

451 shared with genetic inheritance, cultural transmission can be horizontal (within or  
452 between groups, and extending to non-kin), or oblique, with learning from non-relatives  
453 in the prior generation (15). Above I have reviewed some of the evidence for learning  
454 from parents, typically the mother, in apes (38-41, 45). Horizontal and oblique  
455 transmission are commonly demonstrated in diffusion experiments (63-69), as well as in  
456 observational studies in the wild (42-44) and in sanctuaries (34). This makes cultural  
457 learning a powerful adaptive process, as does the fact that because it hinges on neural  
458 rather than genetic changes, it can act very much faster; some important things can even  
459 be learned observationally in a matter of minutes (94), even though complex skills may  
460 require a more extended observational apprenticeship (32, 39).

461       Additionally, whilst adaptive information is inherited genetically in a package at  
462 conception (even if activation is later adaptively contingent on environmental inputs),  
463 that which feeds into social learning can be temporally distributed, in at least two major  
464 ways. First, cultural transmission can be Lamarckian-like, with adaptive features  
465 acquired through one individual's lifetime passed on to those who learn from them.  
466 Second, a learner can progressively build up complex skills such as some forms of ape  
467 tool use, by repeated cycling through a process of observe, practice, observe again and  
468 practice again. This can be thought of as a spiral or helical process of learning in which  
469 cycles of observation and practice allow the learner to assimilate more in later  
470 observations than was possible in the earlier, more naïve stages (32, 39) (Fig. 3).

471

472       < insert Fig. 3 about here >

473

474 Social learning may also be selective in the assimilation of information, variously  
475 referred to as directed social learning (95), biased transmission (15) or social learning  
476 strategies (96), which can in principle shape adaptation and consequent evolutionary  
477 change, with no clear counterparts in the gene-based processes.

478

479 **Selectivity in social learning.** Evidence has been adduced for a number of the potential  
480 learning rules these analyses highlight, in great apes (97). Evidence for a 'copy the  
481 majority' rule, suggested by apparent conformity of chimpanzees in diffusion  
482 experiments (68), came in further experiments showing that both children and



483 chimpanzees would copy the choices of three other conspecifics rather than a single  
484 individual repeating the same act three times (98). Orangutans did not do this (98),  
485 possibly reflecting their less community-based social life. Evidence for discriminating  
486 more successful or productive options and copying these came from further experiments  
487 with chimpanzees (99). It has been suggested that preferentially copying individuals of  
488 high rank could serve this function too, and two studies have shown chimpanzees  
489 preferring to copy a high ranked over a lower ranked individual (100, 101). Finally, a  
490 tendency to learn from kin is shown by the studies of peering reviewed earlier, which  
491 showed extensive learning from the mother during apes' extended pre-weaning period  
492 (39, 41). After weaning, this widened to include peering at the activities of others, a  
493 plausibly adaptive shift from initially learning basic information from parents, then later  
494 targeting others to learn more specific skills, a trend identified in studies of human  
495 children, both observational (102) and experimental (103, 104). However, we still have  
496 only limited understanding of when and why an ape opts to learn socially, or not: for  
497 example, what determines when immigrants will either conform to local norms (30), or  
498 instead transmit their habitual skills to others (44)?

499

## 500 **Interactions between genetic and cultural modes of inheritance and evolution**

501

502 At the broadest level, culture extends biology insofar as some culturally transmitted  
503 behaviors are evolutionarily consequential; they have implications for practitioners'  
504 survival, reproduction and ultimate inclusive fitness (as opposed to the reproductive  
505 success of the cultural items themselves, discussed earlier). This may be less so for  
506 some cultural variants that appear relatively frivolous, such as staring at one's reflection  
507 in water in gorillas (23) or applying an autoerotic tool in orangutans (22), but varied  
508 forms of tool use by orangutans and chimpanzees appear highly functional in gaining  
509 access to rich resources like insect prey, nut kernels and honey. Indeed, some of these  
510 appear vital for chimpanzees to exploit niches that would otherwise exclude them (87).  
511 Other culturally transmitted behaviors play functional roles in grooming, social  
512 interactions and sexual courtship.

513

514 Another sense in which culturally transmitted behaviors may have been evolutionary important concerns their effects on organic evolution. Cetacean researchers

515 have proposed that cultural differentiation among whales has led to genetic differences  
516 (7, 105). For example, killer whales display ‘eco-types’ that specialize in hunting  
517 alternative prey such as seals or fish using very different techniques, and different clans  
518 exhibit other behavioral differences in their songs and migratory/resident patterns,  
519 despite often being sympatric (6, 7, 105, 106). Such effects are suggested to have driven  
520 other morphological and genetic differentiation, ultimately leading to incipient  
521 speciation, for it becomes difficult for a member of one culture to enter another and  
522 successfully manage the different foraging and courtship requirements there. This  
523 would be an instance of ‘behavioral drive’ (107-109), in which plasticity in behavior  
524 allows a species to exploit or create a new niche – in this case a culturally dependent  
525 one (e.g. fish versus seal hunting - hence ‘cultural drive’). This in turn may create  
526 selection pressures acting on organic evolution, with effects such as the evolution of  
527 more robust jaws in the seal-hunters (6). Parallel hypotheses have been developed in the  
528 case of birdsong dialects driving speciation (110-111).

529       Such dramatically different specialisms as in killer whales is not apparent amongst  
530 great apes, although the extent to which there are similar processes at work in contrasts  
531 between, say, nut-cracking communities of chimpanzees, and the nearest neighbors that  
532 do not crack, would repay attention. However, one principal effect of complex culture  
533 on organic evolution in apes has been proposed, concerning encephalization and the  
534 cognitive sophistication it can provide: the Cultural Intelligence Hypothesis.

535

536 **The Cultural Intelligence Hypothesis.** In accord with a previously advanced Social (or  
537 ‘Machiavellian’) Intelligence hypothesis, relative brain size in different primate species  
538 was found to be predicted by the typical size of their social group and the concomitant  
539 demands on social cognition (59, 112). Great apes do not fit this pattern, showing high  
540 relative and absolute brain sizes, yet in the case of gorillas and orangutans, not living in  
541 large communities. However as all appear to display relatively complex cultures, the  
542 Cultural Intelligence Hypothesis suggests this complexity has selected for  
543 encephalization, either in a ‘culture first’ or an entwined culture-gene-brain co-  
544 evolution scenario (112-115). One side of this proposition may be glossed as ‘culture  
545 makes you smart’ - self-evident in the human case (9), insofar as present-day humans  
546 are smarter than a century earlier by virtue of the cumulative cultural achievements

547 from which they benefit. On a more modest scale, the same is proposed for the cultural  
548 endowment of great apes. The converse side of the proposal is that there is selection on  
549 the socio-cognitive capacities necessary to assimilate and store all the potential cultural  
550 repertoire available. In turn, it has been suggested that there will be correlated selection  
551 on technical and general intelligence, so as to benefit from the cultural input, as in  
552 intelligent tool-use, for example (114). One test of such ideas recently offered showed  
553 that when tested on the ‘level playing field’ of Zoo contexts, Sumatran orangutans  
554 scored higher on general intelligence than their Bornean cousins, as predicted by the  
555 more elaborate cultural repertoires of the Sumatran populations in the wild; moreover  
556 Sumatrans have 2-10% larger brain sizes (116).

557

## 558 **Summary and Conclusions**

559

560 Research particularly in the last two decades or so have shown that a ‘second  
561 inheritance system’ of social learning is widespread amongst animals, extending to all  
562 main classes of vertebrate and insects too (1, 2). Apes merit a special focus insofar as  
563 they have been subjected to an unmatched diversity and volume of observational and  
564 experimental studies by multiple research teams, which has revealed what appear to be  
565 the richest non-human cultural repertoires identified to date (although some cetaceans  
566 may show greater cultural *differentiation*, like the killer whales). This article has  
567 attempted to indicate the scope of ape culture research and the key points of its  
568 discoveries, particularly with respect to the theme of the present issue: how these  
569 cultural phenomena may extend biology, and its core evolutionary theory in particular. I  
570 have argued that the evidence supports the conclusion that the nature of social learning  
571 and its consequences in cultural transmission create new forms of evolution, that echo  
572 well established core principles of organic evolution, but also go beyond them in a  
573 number of fundamental ways, such as horizontal transmission and inheritance of  
574 acquired characteristics, thereby extending the scope of evolutionary processes we must  
575 now entertain. Moreover the primary genetically based forms of evolution shaped, and  
576 are also shaped by, the consequences of this second inheritance system, in complex  
577 ways we are only now starting to uncover.

578

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582

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824 Figure captions

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826 Fig. 1. 'Peering' (ref. 39) in a juvenile orangutan as her mother extracts termites from  
827 dead wood. Photo courtesy of Christiaan Conradie and Caroline Schuppli.

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829 Fig. 2. Convergent evidence for a culture of nut-cracking in chimpanzees. Evidence for  
830 nut-cracking at multiple sites in West Africa (20, 21, 60) (white stars) but absent at others  
831 (black stars). Independent studies confirmed availability of raw materials at two such  
832 sites (61, 62). Experiments showed East African chimpanzees did not initially nut-crack  
833 (Phase 1), but half exposed to a proficient model began to do so (Phase 2) and all did  
834 once all so exposed (Phase 3) (31,32).

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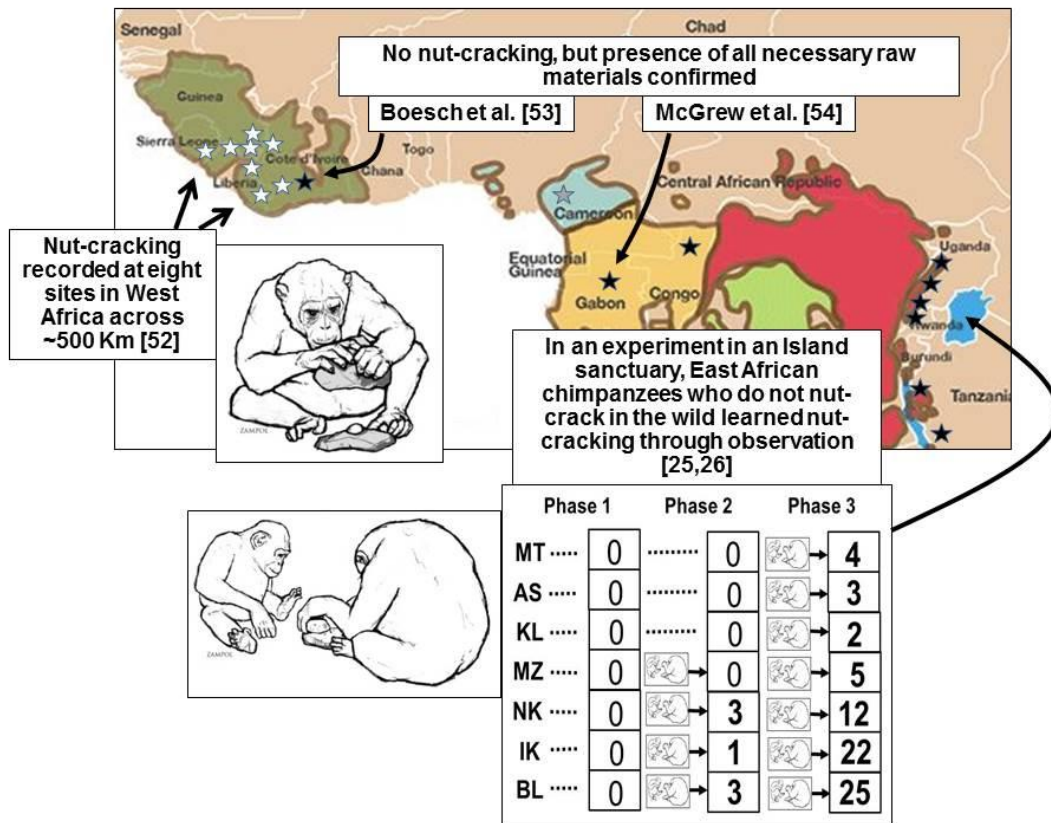
836 Fig. 3. 'Helical Curriculum' model of skill development (after Ref. 32). Over repeated  
837 cycles of observation-of-expert and practice, the social learner is able to assimilate more  
838 information from the expert and gradually improve their skill level. See text for more  
839 explanation.

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