

Social traditions

Lara Wood and Andrew Whiten

This is the accepted manuscript of the book chapter:
Wood, L. and Whiten, A. 2017. Social traditions. In: A. Fuentes, ed.
The International Encyclopedia of Primatology. John Wiley & Sons.

It has been published in final form at doi:
<http://dx.doi.org/10.1002/9781119179313>

Published version © 2017 John Wiley & Sons
<http://eu.wiley.com/WileyCDA/WileyTitle/productCd-0470673370.html>

This chapter may be used for non-commercial purposes in
accordance with the Wiley Terms and Conditions for Self-Archiving



social traditions

Journal:	<i>International Encyclopedia of Primatology</i>
Manuscript ID	PRIM-0251.R1
Wiley - Manuscript type:	Entry
Date Submitted by the Author:	n/a
Complete List of Authors:	Wood, Lara; University of St Andrews, Psychology & Neuroscience Whiten, Andrew; University of St Andrews, Psychology & Neuroscience
Keywords:	Tradition, learning, Cumulative culture, Transmission biases, Conformity
Abstract:	

SCHOLARONE™
Manuscripts

Only

1
2
3
4
5
6
7
8
9
10
11
12
13

Social Traditions

Lara A. Wood and Andrew Whiten

University of St Andrews

This work was supported by grant ID 40128 from the John Templeton Foundation to
K. Laland and A. Whiten.

lanw@st-andrews.ac.uk, aw2@st-andrews.ac.uk

Word Count: 4,638 (Including the main text, and the reference and further reading
sections. Abstract and keywords are not included in the word count.)

For Review Only

14 **Abstract**

15 Social traditions, here defined as displaying inter-group behavioural differences acquired
16 through social learning, have been identified in a number of primate species. Here we review
17 research methods used in the wild and in captivity to identify the presence of both primate
18 social traditions and the necessary social learning mechanisms involved. Moving beyond
19 evidence of the presence of primate social traditions, to their function, longevity, biased
20 transmission, conformity and cumulative nature, allows for the exploration of convergences
21 and divergences between primate and human traditions.

22

23 **Keywords**

24 Tradition, learning, transmission biases, conformity, cumulative culture.

25 A social tradition is a *distinctive* and *persistent* behavioural trait shared by several
26 members of a group. Critically, the spread of this behavioural trait is facilitated by *social*
27 *learning* from one individual to another. Social traditions are not unique to humans and
28 several other primate species demonstrate social traditions, from food processing to social
29 conventions. This article offers an overview of how differing research methods have
30 illuminated the vast array of primate social traditions. Underpinning these traditions are a
31 suite of social learning mechanisms that we summarise and discuss. Moving beyond
32 descriptions of traditions to the identification of variable features such as the function,
33 longevity, selective transmission, and, at times, cumulative nature of primate traditions will
34 highlight convergences and divergences between primate traditions and human culture.

35

36 **Identifying Social Traditions**

37 Varied research methods, including systematic observation, experimental studies and
38 social network analyses, have identified a number of primate social traditions (see Whiten,
39 2012 for a detailed review of methods and studies). One primary method of identifying social
40 traditions within a species is to observe inter-group differences in the behavioural repertoire
41 of the same species. This can be achieved through a collaborative amalgamation of
42 observations at multiple field sites. Comparisons of these observations can highlight
43 behaviour patterns that are common for at least one community yet absent for another, with
44 no discernible genetic or environmental explanation.

45 Such research has been undertaken with two ape species; orang-utans (*Pongo* spp.)
46 and chimpanzees (*Pan troglodytes*). The results demonstrated 30 and 40 such behaviour
47 patterns or traditions respectively, that were habitual in some communities but non-existent in
48 others. For example, use of natural wooden and stone hammer materials to crack open hard
49 nuts is customary in chimpanzee communities over a wide span of far-West Africa, yet

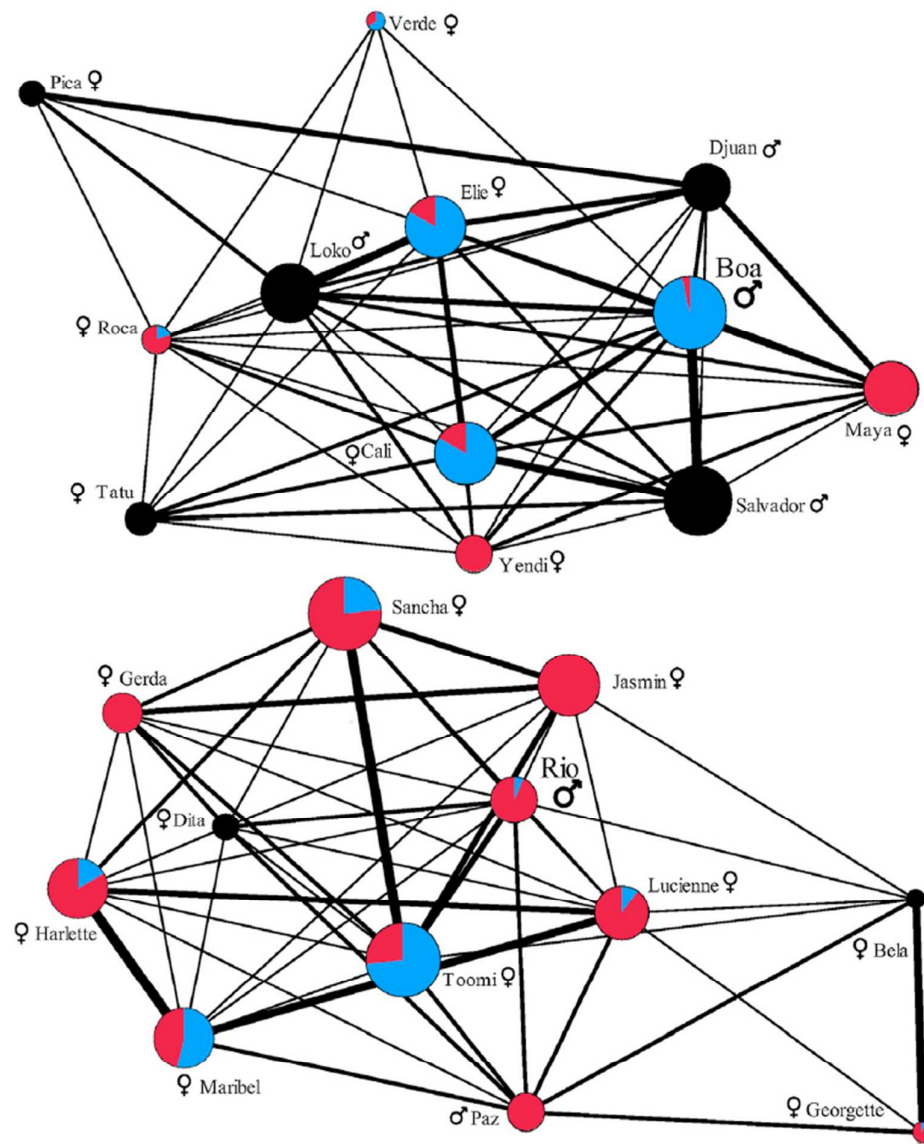
50 absent elsewhere despite the presence of all the raw materials confirmed in separate studies.
51 Recent studies have even demonstrated differences in hammer type preferences in
52 neighbouring communities, making alternatives explanations like genetic or ecological
53 differences, implausible.

54 The large-scale data sets relating to inter-group behavioural differences are
55 importantly complemented by recording a group's acquisition of a tradition 'as it happens'.
56 Hobaiter et al. (2014) tracked the group spread of a moss-sponge drinking innovation by a
57 dominant male chimpanzee while also studying the social dynamics within the community
58 through the use of social network analysis. Social network analysis maps the strength of
59 relationships between group members. Dynamic network-based diffusion analysis, which
60 quantifies the extent to which the spread of a new behaviour is consistent with a *repeatedly*
61 updated social network, led to the discovery that each time a novice observed an existing
62 moss-sponger there was a 15-fold enhancement of moss sponging behaviour for that
63 observer. These findings are valuable evidence of group traditions in chimpanzees, although
64 purely observational studies of natural behaviour are correlational and care is necessary in
65 inferring causation in such approaches.

66 Moving beyond observation and correlation to controlled experimentation which can
67 reliably identify causation can further our understanding of primate social traditions. Target
68 behaviours may be artificially created (by training models), seeded and manipulated in order
69 to examine whether the seeded behaviour transmits across the group and, if so, the
70 mechanisms of this transfer. Triangulating experimental manipulations of behaviours with
71 observations allows for an even more detailed description. Claidiere, Messer, Hoppitt., &
72 Whiten (2013) seeded foraging behaviours in two groups of squirrel monkeys housed in
73 identical enclosures within a zoo. The alpha male in each group was trained to remove food
74 from a puzzle using one of two different methods. The males then demonstrated their

75 respective method to the rest of the group, after which all members of the group had access to
76 the task. Additionally, each monkey's total time spent in the experimental zone was coded
77 dependent on whether they were alone or with specific conspecifics. This created a social
78 network analysis where the network centrality of an individual, which increases with the
79 strength of its social connections, was calculated. Results showed that the two techniques
80 spread preferentially in the groups in which they were initially seeded. Furthermore, network
81 centrality predicted both the speed with which an individual would first succeed in opening
82 the artificial fruit and the probability that they would acquire the method seeded in their
83 group (see Figure 1). These findings demonstrate how important social relationships can be in
84 the spread of social traditions.

85 These various research methods demonstrate that (1) there are enduring group
86 differences in behaviours among some wild populations of primates; (2) experimentally
87 seeded behaviours can spread among a group creating micro-traditions; and (3) there is a
88 relationship between social dynamics and social learning. We now focus on how behaviours
89 may spread to create traditions by focussing on social learning mechanisms.



90

91 *Fig. 1. Sociograms illustrating cultural diffusion in two groups of squirrel monkeys. Boa*
 92 *(top) was trained to use foraging method 1 (blue) and Rio was trained to use method 2 (pink).*
 93 *Link size is proportional to bond strength. Node size is proportional to the network centrality.*
 94 *Node colour indicates the actions performed by each monkey: the pie chart represents the*
 95 *proportion of method 1 (blue) and method 2 (red) for a maximum of 30 successes: a black*
 96 *node represents individuals that were unsuccessful. Figure reproduced from Claidiere et al.*
 97 *(2013)*

98

99 **Social Learning Mechanisms**

100 By definition, social traditions rely on social learning; learning by observation of
101 another individual or its products. How this learning happens can vary dramatically both
102 within and between species. Identifying the mechanisms involved in social learning through
103 observing wild populations is challenging because shared behaviour among individuals does
104 not necessarily imply social learning and observation does not identify exactly *how*
105 behaviours may have been socially learned. Thus, experiments have proved a more fruitful
106 avenue of research. These experiments tend to focus on the use of artificially seeded
107 behaviour as with the captive squirrel monkeys described above (Claidiere et al., 2013).
108 Researchers can create artificial challenges involving the acquisition of food, akin to
109 accessing fruit within a natural shell ('artificial-fruit' tasks). Typically, an individual will
110 learn by exploration, or be trained, to access the food using a particular method, while an
111 alternative method is blocked. This individual then performs the behaviour in the presence of
112 one (dyadic approach) or more ('open' diffusion approach) individuals over a period of time.
113 Critically, scientists can then look beyond simple measures such as success or failure in
114 acquiring the food and look at the specific acquisition methods.

115 These social learning experiments have been conducted successfully with an ever-
116 growing number of primate species both in the wild and captivity, using a range of methods
117 (dyads, chains of dyads and open-diffusion), observational methods (live and video) and
118 different tasks. While these studies might not necessarily demonstrate the *persistence* of
119 behaviour required in traditions they shed light on the process of social learning. For
120 example, open-diffusion artificial-fruit experiments with humans, chimpanzees, vervet
121 monkeys, capuchins, marmosets, squirrel monkeys and lemurs (see Schnoell et al, 2014 for
122 the latter example) have shown that different groups, seeded with different methods of

123 extracting rewards, will show a group-level preference for the seeded method. Thus, these
124 species demonstrate the cognitive skills and social learning mechanisms necessary to sustain
125 social traditions across different communities, including quite complex variations in foraging
126 techniques.

127 These kinds of experiments can be extended to shed further light on learning
128 mechanisms. For example, an experimenter can manipulate the task by some hidden means,
129 resulting in the same task movement as with a live model. This ‘ghost’ control method allows
130 for a distinction between object or body movement re-enactment. If a species copies a
131 method equally well with or without a model then it may be that they are socially learning
132 through ‘object movement re-enactment’, but this says nothing of whether they can copy
133 another’s actions towards a task. When a task is relatively easy, chimpanzees will initially
134 copy the extraction method, whether demonstrated by a model or a ‘ghost’ wire pulled by the
135 experimenter. However, fidelity to this method is much higher when a model demonstrates
136 the method. Furthermore, with a harder task, chimpanzees were unable to learn an artificial-
137 fruits retrieval method through a ghost display even though they could when modelled by a
138 conspecific (Hopper et al., 2008). This suggests that the presence and specific movements of
139 a model are important to the observer and suggests body movement re-enactment, or
140 imitation, is present in chimpanzees. However, it has been argued that primates tend to copy
141 only some aspects of a given behaviour, and precise information regarding actions is not so
142 readily transmitted, leading to cultural ‘slippage’. In contrast, from a very young age humans
143 tend to copy actions, end results, and goals and show much higher fidelity copying, at times
144 resulting in the persistent copying of causally irrelevant or inefficient actions. Humans,
145 however, are not the only species that socially learn behaviours with opaque functions, as
146 explained in the following section.

147

148 **Functions of Social Learning**

149 In research on human copying, a distinction has been made between copying to learn
150 new skills or deal with the physical environment (informative or instrumental context), and
151 copying that might serve a social function (normative context). This difference could lead to
152 two quite different types of social traditions. Thus, while the function of some copying might
153 be to identify useful information about the environment, the function of normative cases
154 might be to align oneself with a behaviour shared socially by a group, which in turn may
155 serve the function of facilitating social relationships.

156 Thus far we have cited examples of primate social traditions that have an obvious
157 function; methods of handling or acquiring food or water. Such social traditions have an
158 obvious evolutionary advantage for individuals who can thus benefit from the innovations of
159 group members, potentially innovations created many generations before. Indeed, 19 of 40
160 examples of social traditions found in the wild chimpanzees related to food or drink handling
161 or acquisition. Other social traditions identified also had a relatively obvious advantage, such
162 as one group's habitual behaviour of placing large leaves on the ground for sitting on, as an
163 apparent protection from the wet ground. These social traditions can serve to inform naïve
164 individuals about their physical environment.

165 Conversely, other social traditions identified in the chimpanzee groups did not inform
166 individuals about the physical environment and thus have a more opaque function. For
167 example, the same group of leaf-sitting chimpanzees showed a distinct method of grooming
168 whereby the two grooming individuals clasped hands overhead and groomed each other with
169 the other hand. While grooming behaviour is species-typical and is thought to strengthen
170 social bonds, the specific style of the clasped hands seems arbitrary. This hand-clasp tradition
171 was absent in other groups although these groups also possessed intra-group behaviours with
172 less obvious functions. Inter-group differences in social interaction seem akin to human

173 cross-cultural differences in conventions like greetings involving handshakes, cheek kissing,
174 bowing and embracing. Thus these traditions may have a normative rather than informational
175 function.

176 Apes are not alone in demonstrating social traditions that do not function to improve
177 interactions with the physical environment. Groups of Japanese macaques (*Macaca fuscata*)
178 have developed and transmitted solitary “play” behaviours of manipulating multiple stones.
179 The way in which these stones are played with also varies from group to group. Likewise, a
180 23-year observation of white-faced capuchins (*Cebus capucinus*) led by Susan Perry
181 identified social conventions with potentially dangerous side effects (Perry et al., 2011). As
182 well as hand sniffing and sucking of body parts, researchers identified “games” initiated in a
183 play context. The most extreme example of this is “eye-poking” whereby a monkey inserts a
184 partner’s finger into his own eye socket up to the first knuckle. Such a game surely carries the
185 risk of damaging the eye and so raises questions as to the function or benefit of such a
186 behaviour. Perry hypothesizes that these dyadic interactions help test and perhaps display the
187 quality of the social relationship. Therefore, a risky tradition reliant on a close social bond
188 serves an important function in another primate species where social bonds are key.

189

190 **Longevity**

191 By their very definition social traditions are persistent, but the length of this
192 persistence inevitably varies between traditions. Understanding the longevity of a tradition
193 might help us to understand the transmission and function of any socially learned behaviour
194 pattern. There is archaeological evidence that nut cracking in chimpanzees using stone
195 hammers was present over 4,000 years ago in West Africa. Fragments of the same nuts eaten
196 by present day chimpanzees were found on the stone tools. This supports other evidence that
197 the behaviour of nut cracking is a persistent social tradition.

198 Conversely, some social traditions already described were invented, transmitted and
199 then expired within the time the group was being observed. Susan Perry wrote that, among
200 the wild capuchins that she observed over many years, the most remarkable thing about the
201 seemingly non-adaptive but socially important social customs was the number of apparent
202 extinctions of traditions observed in a relatively short time. For example, hand sniffing died
203 out in several groups after just a few years of observation. Such short-lived traditions may be
204 seen as akin to human fashions and fads in which a behaviour develops among a population
205 and is transmitted enthusiastically for a period of time, before fading quickly. An obvious
206 example of a human fads is fashion in the way we use materials to adorn our bodies. Similar
207 behaviour of adorning bodies with a material has been observed in one of four groups of
208 chimpanzees housed in a sanctuary in East Africa. Specifically, chimpanzees selected a stiff,
209 straw-like blade of grass, inserted the grass into one of their own ears, adjusted the position,
210 and then left it in their ear during subsequent activities (van Leeuwen, Cronin, & Haun,
211 2014).

212 Perry speculates that the short life of the capuchin traditions might be due to group
213 instability or the difficulty of preserving traditions that require an understanding of two roles,
214 or due to the death of the initiator of the behaviour. Another possibility is that social
215 traditions with an instrumental function may persevere longer than traditions with a social or
216 normative function. To date there has been little experimental work on investigating what
217 affects the longevity of social traditions. Social learning experiments involving two
218 individuals can only show short-term instances of social learning. A diffusion experimental
219 design, where there are multiple chances for information transfer between numerous
220 individuals, allows for seeded behaviour to be studied over a somewhat longer period of time.
221 Primate diffusion experiments involving artificial fruits have shown relative perseverance of
222 the seeded behaviour. The removal of a reward from a task represents an instrumental context

223 and so one might expect only the instrumental actions to persevere over generations.
224 Diffusion experiments seeding with functionally irrelevant behaviour is far rarer and thus far
225 only seen with humans. For example, Flynn (2008) investigated children's copying of actions
226 that have no obvious function through a diffusion chain (child A models for child B who then
227 models for child C and so on). The initial child in each chain performed a series of actions on
228 an artificial fruit task in order to retrieve a reward. Some actions were instrumental in
229 removing the reward whereas some actions were functionless. Children showed initial fidelity
230 to the precise action that had the function of removing the reward. However, the actions that
231 did not function to remove the reward were parsed out in the diffusion chains over multiple
232 "generations". These results support the notion that there might be a relationship between a
233 function of a social tradition and the longevity of this tradition. This is an area ripe for further
234 exploration.

235

236 **Model-based biased transmission**

237 In the previous sections we reviewed tentative evidence that the function of a
238 behaviour or tradition might affect its transmission. These are examples of how social
239 traditions may be shaped by social learning biases or strategies that dictate the circumstances
240 under which primates copy others. These strategies allow an individual to counteract the risk
241 in social learning, of potentially acquiring outdated or maladaptive information. These biases
242 also likely play a crucial role in determining how behavioural variants are spread and
243 maintained at population levels. One social learning bias posits that the identity of the
244 innovator of a particular behavior, or the users of a long-standing behavior, may influence the
245 persistence of a social tradition. Such biases are model-based social learning biases.

246 Longitudinal observations of the acquisition of tool-based termite fishing in
247 chimpanzees has shown that young females spend significantly more time observing their

248 termite-fishing mothers than young males. These females successfully termite-fished around
249 two years earlier than young males and the techniques of female offspring closely resembled
250 those of their mothers. The close proximity of the mother and female offspring certainly gave
251 the young females the opportunity to socially learn the behaviour. This observation is based
252 on correlation so inference of causation must be guarded, but it suggests that if two equally
253 viable behaviours were invented by a mother or another individual, the mother's behaviour
254 would more likely be adopted by female offspring, and potentially other members of the
255 group. Increased observation of particular individuals has also been found with capuchin
256 monkeys that attend more to successful conspecifics.

257 Kendal and colleagues (2015) gave four captive groups of chimpanzees a novel
258 extractive foraging device and tracked the adoption of two methods of reward- retrieval. The
259 groups showed evidence of method preference although every group discovered both
260 methods. Investigating competence and rank, the researchers used statistical models to
261 provide evidence of model-based biases in the transmission of the method choice.
262 Chimpanzees that had not yet had success with the task tended to choose to observe
263 individuals of a higher rank or trained demonstrators (as in two of the groups) more than
264 those of the same rank. However, high-ranking individuals rarely showed fidelity to one
265 method and were not prone to watching social information. The authors speculate that this
266 pattern of copying, biased towards a high-ranking model who does not seem prone to social
267 learning themselves, may explain why high innovation rates among low rank individuals do
268 not generate a correspondingly high frequency of traditions in chimpanzees. Again, this sort
269 of research is in its infancy and is hampered by issues of dominance or monopolization of
270 resources within primate populations.

271

272 **Migration and Conformity**

273 The pervasiveness of a social tradition may lead individuals to change existing
274 behaviour to that of the majority group behaviour. Such a change represents another example
275 of biased transmission and can be seen as a form of conformity. An effective way of
276 observing conformity in the wild is to track individuals migrating from one group to another.
277 Van de Waal, Borgeaud, & Whiten (2013) presented four groups of wild vervet monkeys
278 with two adjacent trays of maize corn. One tray contained normal tasting corn dyed one
279 colour and another tray contained highly distasteful corn dyed an alternative colour. The
280 monkeys soon learned to avoid the distasteful coloured corn. The trays were removed for
281 several months in which time 10 males moved to a group that preferred the alternative
282 coloured food to that eaten in their original group. When the trays were returned, both now
283 tasted normal. After observing others feeding there, the first choice of seven of these males
284 was for the locally preferred corn which was previously the distasteful option for them. None
285 of the resident males ate the colour corn that was previously distasteful. A further two
286 ‘immigrants’ adopted the new group’s behaviour once higher ranking animals moved away
287 from the preferred food. The only male that continued to eat the same colour as in his original
288 group immediately took the top rank in his new group, a factor that may have influenced his
289 behaviour. Understanding conformity to an individual’s new group will add considerably to
290 our understanding of cultural transmission in animals. For example as noted earlier,
291 observations in the wild showing that migrating female chimpanzees assimilate their new
292 group’s behaviours (Luncz & Boesch, 2014) might explain the observed maintenance of
293 distinct cultural repertoires in neighbouring communities.

294 Considering the link between the function of a social tradition and the motivation for
295 conformity is important. For the migrating vervet monkeys, conformity to the new group
296 might represent informational conformity whereby the information provided by the new

297 group provides environment-specific information about the best food source. Alternatively,
298 the migrants may be more concerned about adopting the behavior of the new group for social
299 reasons such as creating affiliative bonds or adhering to group norms. This is termed
300 normative conformity. Certainly, the one male that maintained his old group norm while
301 becoming the new group's dominant male indicates that there may be something more
302 complex than just informational conformity occurring. Normative conformity is a well-
303 documented human phenomenon. But finding direct evidence for normative rather than
304 informational conformity would, again, be challenging with primate populations.
305



306
307 **Fig. 2.** Vervet monkeys eating coloured corn. Here, an infant (left) sits on the colour earlier
308 made distasteful to its mother (before it was weaned), as it eats the colour currently preferred
309 by its mother and the rest of the group. Photo from van de Waal et al. (2013).

310

311 **Divergences with Humans**

312 Humans and several other primate species show convergence in (1) group level
313 behavioural differences indicative of social traditions; (2) the ability to socially learn these
314 behaviours; (3) the presence of both instrumental and social traditions; (4) biased
315 transmission of social traditions; and (5) migratory flexible behaviour change allowing
316 behaviour matching with a new social group. With all this convergence, the question remains
317 as to why there is still such an obvious disparity between humans and primates in terms of the
318 breadth, complexity and evolution of social traditions.

319 While some might define culture as synonymous with social traditions insofar as both
320 display distinctive and persistent socially learned group behavioural traits, human culture
321 possesses characteristics that animal culture lacks. While animal traditions and human culture
322 provide naive individuals with a means of acquiring adaptive behavioural innovations, human
323 culture demonstrates traditions across a richer range of behavioral domains and serves
324 functions never seen in animal traditions. Thus, human culture is divergent from primate
325 traditions, for only humans appear to assimilate socially learned traits that function as
326 markers of shared group membership and result in communal understanding of group-
327 appropriate behaviour.

328 When research focuses on the function of social traditions, human and animal
329 traditions are seen as more similar than when studies focus on the mechanisms of acquiring
330 social traditions. Emerging research suggests that human culture is dependent on
331 psychological processes that are either absent or severely limited in apes. As previously
332 noted, humans appear to show higher fidelity copying than other primates. This difference,
333 along with other socio-cognitive skills, typically seen in humans but absent in other animals,
334 could have the potential to affect the complexity and efficacy of social transmission of
335 information.

336 Dean et al. (2012) presented children and captive groups of chimpanzees and
337 capuchins with a multi-step artificial-fruits task, where completion of each of three stages
338 increased reward value. The capuchins and chimpanzees generally struggled to get beyond
339 stage 1, and individuals failed to learn from the few individuals that did reach higher stages.
340 In contrast, the majority of the groups of children reached the final stage and their
341 performance corresponded with a number of other behaviours not seen in the chimpanzees or
342 capuchins. These included high fidelity copying and pro-social behaviour from the model
343 including pro-sociality (reward sharing), communication and active teaching.

344 This suite of socio-cognitive skills meant that at the group level there was high
345 fidelity copying but also a progression of success on the task. A cycle of high fidelity copying
346 alongside improvement leads to what is commonly known as the ratchet effect, which tends
347 to prevent the slippage of innovations and social traditions discussed earlier. Such a cycle is
348 thought to be responsible for the important human phenomenon of cumulative culture,
349 whereby the complexity or efficiency of cultural traits are enhanced over repeated
350 transmissions. Cumulative culture creates behaviours and technologies that could not have
351 been invented by a single individual in his/her lifetime.

352 To date, there is very little evidence for cumulative culture in any species besides
353 humans and any evidence is often controversial. When possible behaviour modifications have
354 been identified in the wild these modifications are not always more complex nor more
355 efficient than previous behaviours, nor such that one individual could not have invented them
356 alone. Likewise, direct empirical investigation of cumulative culture in primates has often
357 shown conservatism to original solutions and thus an inability to move to more complex or
358 efficient behaviour. Furthermore there is only very limited evidence that any modifications
359 move beyond what an individual could invent for themselves. Thus to date, substantial
360 cumulative culture appears to be a uniquely human characteristic.

361

362 **Conclusion**

363 Primate social traditions have been identified in a number of Old-World and New-World
364 monkeys, and in great apes. These animals demonstrate a cognitive capacity for social
365 learning as well as the presence of distinct and persistent inter-group behavioural differences.
366 Such traditions share many features with human traditions such as variation in function,
367 longevity, biased transmission and plasticity, although the exact nature of these features may
368 also often differ between humans and other primates. There remains a huge gulf between
369 primate traditions and human culture due to the volume, persistence and cumulative nature of
370 human culture, but the evidence for primate culture reviewed here indicates that human
371 culture did not spring out of nowhere; it has substantial roots in earlier phases of primate
372 evolution

373 **References**

- 374 Claidiere, Nicolas, Emily, J.E. Messer, William Hoppitt, and Andrew Whiten. 2013.
375 "Diffusion dynamics of socially learned foraging techniques in squirrel monkeys."
376 *Current Biology*, 2: 1251-1255.
- 377 Dean, Lewis. G, Rachel, L. Kendal, & Steven Schapiro, Bernard Thierry and Kevin N.
378 Laland. 2012. "Identification of the social and cognitive processes underlying human
379 cumulative culture." *Science*, 3356072: 1114-1118.
- 380 Flynn, Emma. 2008. "Investigating children as cultural magnets: do young children transmit
381 redundant information along diffusion chains?" *Philosophical Transactions of the*
382 *Royal Society B: Biological Sciences*, 363: 3541-3551.
- 383 Hobaiter, Catherine, Timothee Poisot, Klaus Zuberbühler, William Hoppitt, and Thibaud
384 Gruber. 2014. "Social network analysis shows direct evidence for social transmission
385 of tool use in wild chimpanzees." *PLoS Biology*, 12: e1001960.
- 386 Hopper, Lydia. M., Susan P. Lambeth, Steven. J Schapiro, and Andrew Whiten. 2008.
387 "Observational learning in chimpanzees and children studied through 'ghost'
388 conditions." *Proceedings of the Royal Society of London B: Biological Sciences*, 275:
389 835-840.
- 390 Kendal, Rachel. L, Lydia M. Hopper, Andrews Whiten, Sarah F. Brosnan, Susan P. Lambeth,
391 Steven J. Schapiro, and William Hoppitt. 2015. "Chimpanzees copy dominant and
392 knowledgeable individuals: implications for cultural diversity." *Evolution & Human*
393 *Behaviour*, 36: 65-72.
- 394 Luncz, Lydia V. and Christophe Boesch. 2014. "Tradition over trend: Neighboring
395 chimpanzee communities maintain differences in cultural behavior despite frequent
396 immigration of adult females." *American Journal of Primatology*, 76:649-657.
- 397 Perry, S. (2011). Social traditions and social learning in capuchin monkeys
398 (Cebus). *Philosophical Transactions of the Royal Society B: Biological*
399 *Sciences*, 366(1567), 988-996.
- 400 Schnoell, Anna V, Marie T. Dittmann, and Claudai Fichtel. 2014. Human-introduced long-
401 term traditions in wild redfronted lemurs? *Animal Cognition*, 17:45-54.
- 402 van de Waal, Erica., Christele Borgeaud, and Andrew Whiten. 2013. "Potent social learning
403 and conformity shape a wild primate's foraging decisions." *Science*, 340:483-485.

404 van Leeuwen, Edwin. J., Katherine Cronin and Daniel Haun. 2014. "A group-specific
405 arbitrary tradition in chimpanzees (*Pan troglodytes*)." *Animal Cognition*, 17:1421-
406 1425.

407 Whiten, Andrew. 2012. "Social Learning, Traditions, and Culture." In *The Evolution of*
408 *Primate Societies*, edited by John C Mitani, Josep Call, Peter M Kappeler, Ryne A
409 Palombit and Joan B Silk. Chicago: University of Chicago Press.

410

411 **Further Reading**

412 Galef, Bennett. G. (2012). Social learning and traditions in animals: evidence, definitions,
413 and relationship to human culture. *Wiley Interdisciplinary Reviews: Cognitive*
414 *Science*, 3.6: 581-592.

415 Hoppitt, William., & Kevin N. Laland. 2013. *Social Learning: An Introduction to*
416 *Mechanisms, Methods and Models*. Princeton: Princeton University Press.

417 Laland, Kevin. N., & Bennett G. Galef, eds. 2009. *The Question of Animal Culture*. Harvard
418 University Press.

419 Whiten, A., Hinde, R. A., Stringer, C. B. & Laland, K. N. (Eds.) (2012) *Culture Evolves*.
420 Oxford University Press.

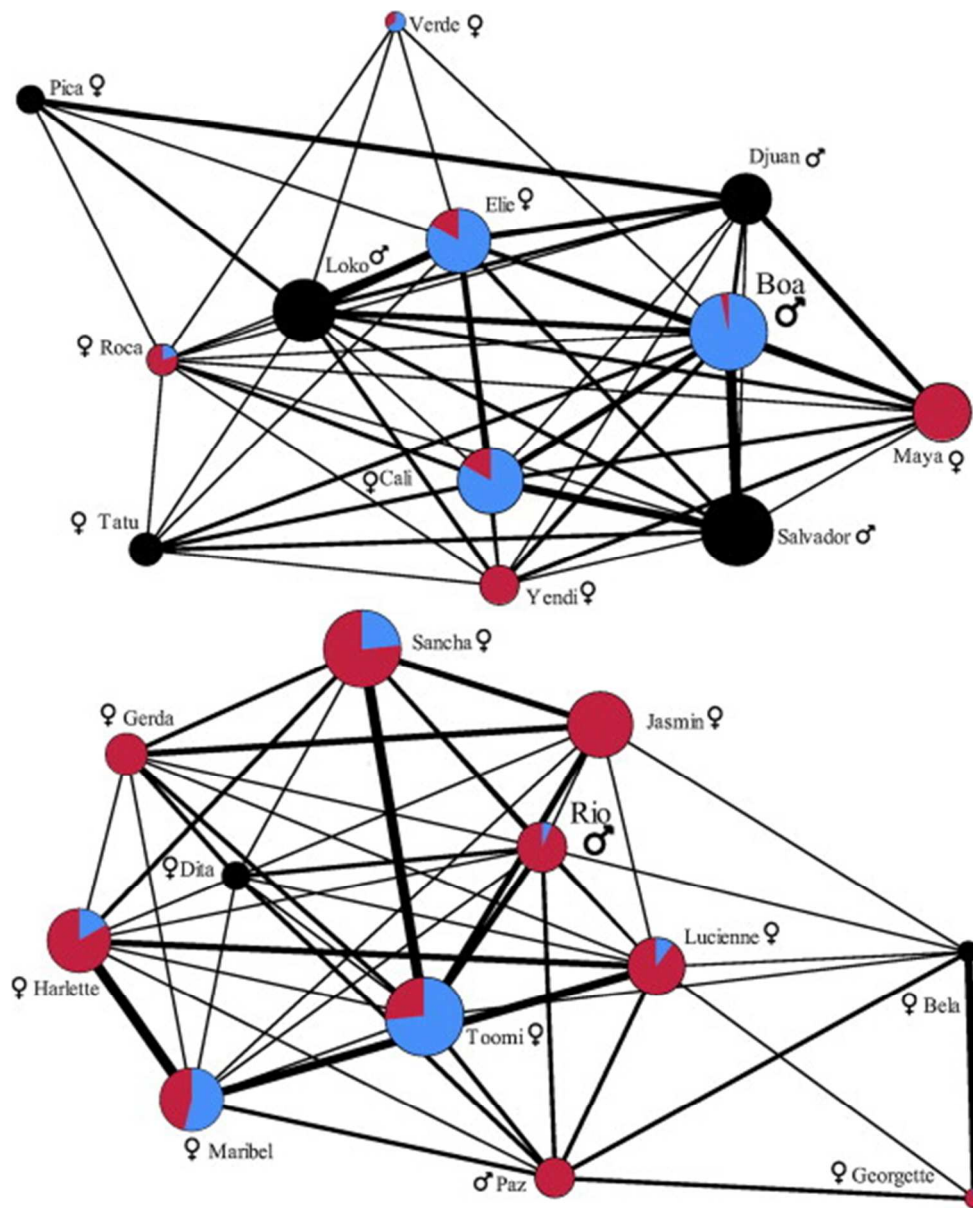


Fig. 1. Sociograms illustrating cultural diffusion in two groups of squirrel monkeys. Boa (top) was trained to use foraging method 1 (blue) and Rio was trained to use method 2 (pink). Link size is proportional to bond strength. Node size is proportional to the network centrality. Node colour indicates the actions performed by each monkey: the pie chart represents the proportion of method 1 (blue) and method 2 (red) for a maximum of 30 successes: a black node represents individuals that were unsuccessful. Figure reproduced from Claidiere et al. (2013)
113x139mm (113 x 113 DPI)



Fig. 2. Vervet monkeys eating coloured corn. Here, an infant (left) sits on the colour earlier made distasteful to its mother (before it was weaned), as it eats the colour currently preferred by its mother and the rest of the group. Photo from van de Waal et al. (2013).
392x260mm (96 x 96 DPI)