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6   **The pervasive role of social learning in primate lifetime development**

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Abstract

In recent decades, an accelerating research effort has exploited a substantial diversity of methodologies to garner mounting evidence for social learning and culture in many species of primate. As in humans, the evidence suggests that the juvenile phases of non-human primates' lives represent a period of particular intensity in adaptive learning from others, yet the relevant research remains scattered in the literature. Accordingly, we here offer what we believe to be the first substantial collation and review of this body of work and its implications for the lifetime behavioral ecology of primates. We divide our analysis into three main phases: a first phase of learning focused on primary attachment figures, typically the mother; a second phase of selective learning from a widening array of group members, including some with expertise that the primary figures may lack; and a third phase following later dispersal, when a migrant individual encounters new ecological and social circumstances about which the existing residents possess expertise that can be learned from. Collating a diversity of discoveries about this lifetime process leads us to conclude that social learning pervades primate ontogenetic development, importantly shaping locally adaptive knowledge and skills that span multiple aspects of the behavioral repertoire.

41 **Introduction**

42

43 Social learning and culture (Table 1) have been studied in non-human primates since the

44 middle of the last century. A substantial scientific literature delineating these

45 phenomena has since accumulated, spanning a diversity of vertebrate species including

46 mammals, birds and fish (Hoppitt and Laland 2013; Whitehead and Rendell 2015;

47 Whiten 2017a) as well as insects and other invertebrates (Grüter and Leadbeater 2015).

48 Primatology has often led the way in these advances, and in the present century has

49 delivered a new range and depth of understanding in this field, supported by a diversity

50 of innovative methodologies (discussed further below). These have often delivered

51 satisfyingly convergent conclusions (Whiten 2012; Watson et al. 2018, for reviews),

52 although there is also ample debate about the exact nature and distribution of the varied

53 forms of social learning across different animal species (Tennie et al. 2009; Whiten et

54 al. 2009; van Leeuwen and Haun 2014; Galef and Whiten 2017; Henrich and Tennie

55 2017).

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57 *** please insert Table 1 about here ***

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59   In the case of cetaceans, Whitehead and Rendell's (2015) comprehensive review

60 concluded that "Culture … is a major part of what the whales are" (p. 7). In other

61 words, culture is inferred to pervade the lives of the whales that these authors study,

62 shaping so much of their behavioral repertoires that their lives would be drastically

63 different if social learning did not play such an influential role in shaping adaptive

64 behaviors. Whiten (2017b) made a similar case for the cultural lives of the great apes. In

65 the present article, we review the evidence bearing on more specific hypotheses: that

66 social learning progressively pervades the infant and juvenile phases of primates' lives;

67 and that it recurs to play an important role in later life events too, notably when

68 individuals mature and disperse to new groups.

69   Our use of the term 'pervades' includes a suite of hypothesized effects: (i) that

70 much of the behavioral repertoire is adaptively shaped by learning from others; (ii) that

71 this spans multiple behavioral domains, from foraging to social behavior; and (iii) that

72 effects may span multiple consecutive generations of traditions acquired by juveniles.

The main body of this review addresses these issues below. In the remainder of this introductory section we indicate the principal outlines of what has been learned about primate social learning and culture more generally, within which the particular dimension of ontogenetic development is to be situated.

Our understanding of this field has been enriched and strengthened by the application of a growing variety of methodological approaches to a widening database of primate species. One important 'broad-brush' starting point has been to compare geographically separated communities of the same species, identifying behavioral differences that through exclusion of any apparent genetic or immediate environmental explanations, are ascribed to cultural transmission. This approach has now identified multiple putative traditions in all the great ape genera (Whiten et al. 1999; van Schaik et al. 2003; Robbins et al. 2016) and in several genera of monkeys (Panger et al. 2002; Leca et al. 2007; Santorelli et al. 2011). More recently this approach has focused more minutely on differences between neighboring communities of the same species both in enclosures in sanctuaries (van Leeuwen et al. 2012, 2014) and in the wild (Luncz and Boesch 2014), thereby further minimizing the possibility that the behavioral differences identified are caused by genetic or ecological variation.

Such conclusions have been reinforced by 'diffusion experiments' in which alternative techniques to deal with the same foraging task have been seeded in individuals acting as potential models in each of two or more groups, and the subsequent differential spread of these documented, again in both apes (Whiten et al. 2005) and monkeys, both in captivity (Dindo et al. 2009) and in the wild (Gunhold et al. 2014; van de Waal et al. 2015). These experiments confirm a capacity for the transmission and spread of innovations through social learning. Sophisticated statistical approaches delineating social networks have also been used to trace the diffusion of naturally occurring innovations along lines predicted by social relationships (Hobaiter et al. 2014). Transmission across multiple generations has been documented by archaeological evidence of nut-cracking excavated deep beneath the surface where the practice continues today, corresponding to over 4,300 years for chimpanzees (Mercader et al. 2007; see Fig. 2 in Whiten 2017a) and 700 years for capuchins (Haslam et al. 2016). These studies have been complemented by diffusion experiments run along a chain of individuals where having learned from A, individual B becomes the model for

105 C and so on, thus simulating repeated inter-generational transfer in these genera (Horner

106 et al. 2006; Dindo et al. 2011). Further extensive series of experiments have probed the

107 particular social learning processes or mechanisms employed by monkeys and apes,

108 often focusing on those that appear the most cognitively challenging, notably emulation,

109 imitation and teaching (Table 1) (Voelkl and Huber 2000; Subiaul et al. 2004; Call et al.

110 2005; Dell'mour et al. 2009; Whiten et al. 2009; Hopper 2010; Tennie et al. 2010; van

111 de Waal and Whiten 2012; Galef and Whiten 2017). More recent developments have

112 begun to address selective, adaptive biases in whom to copy, and when (Haun et al.

113 2012; Price et al. 2017), as well as the constraints imposed by factors such as the

114 relative rank and tolerance of different models and potential learners (Lonsdorf et al.

115 2016).

116   In sum, a substantial diversity of methodological approaches has been applied to a

117 growing array of species across the primate order. The now voluminous primate social

118 learning literature, of which the above cited papers offer but an illustrative sample, have

119 demonstrated a significant role for social learning across many behavioral domains,

120 including diet choice, foraging techniques, tool use, predator avoidance, grooming

121 styles, courtship gambits, vocal communication and reconciliation behavior, plus cross-

122 generation transmission of local traditions.

123   Within this body of work, attention to developmental dimensions has been just one

124 component. However, we believe sufficient material has now accumulated in diverse

125 pockets of the primate literature to merit and sustain what we believe is the first wide-

126 ranging review of the field, complementing an earlier developmental review focused

127 only on the great apes (Russon 2003). We structure this review in relation to three major

128 phases we suggest can usefully be distinguished in the ontogenetic course of social

129 learning as it unfolds in a majority of primates, illustrated in Fig. 1.

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131 *** please insert Figure 1 near here ***

132

133 **The first phase of social learning: 'mother* knows best'**

134 **(*and sometimes other primary caretakers)**

135

136   In most species of monkeys and apes, mothers initially carry and breastfeed their

137   infants. This appears a common pattern in primates, although it is not true of all: for

138   example in callitrichids infants may be predominantly carried by the father and other

139   family members (a topic treated further below); and some Strepsirrhine primates

140   initially leave the infant in a nest. Nevertheless, in the majority of primates maternal

141   care and carriage is initially the norm, even if the extent to which maternal interactions

142   dominate and thus shape opportunities for social learning varies. One extreme is well

143   illustrated by orangutans, whose typical, semi-solitary social structure means that for as

144   much as the first 10 years or so, the mother is the primary and frequently only model for

145   social learning, sometimes with the accompaniment of an elder sibling (van Noordwijk

146   et al. 2009). Juveniles spend most of their time in the same tree as their mother until

147   they are 6-8 years of age. Even for infant chimpanzees, who will typically experience a

148   greater variety of conspecifics in small fission-fusion parties, a majority of their time

149   will be spent in a focused relationship with their mother. By the age of 4 years they are

150   still spending most of their time within 3 meters of their mother and only around 6%

151   (males) or 3% (females) of their time travelling independently beyond 15 meters

152   (Lonsdorf et al. 2014).

153   Some of the most detailed observational studies of this phase have been achieved in

154   the context of the relatively exclusive mother infant relationship of orangutans,

155   mentioned above. For example Jaeggi et al. (2008) tested whether the principal function

156   of mother-offspring food-sharing is (a) to provide nutrition, or (b) to gain adaptive

157   information about foraging. The authors concluded that their results favored the

158   informational hypothesis, because sharing failed to peak at weaning as the nutritional

159   hypothesis would predict; the article was accordingly entitled 'begging for information'.

160   Jaeggi et al. (2010) additionally recorded substantial variance in the diets of multiple

161   mothers, with the dietary profiles of infants found to be essentially identical to their

162   mothers' profiles; immature individuals focused attention on the most difficult of the

163   mothers' techniques, and then tended to practice this rather than manipulating other

164   objects, indicating observational learning of the skills involved. Schuppli et al. (2016)

165   labeled such focused visual attention 'peering', in which an infant may bring their face

166   up close to the activity of interest. Building on the studies by Jaeggi et al. (2008, 2010),

167   Schuppli et al. showed that a quantitative index of the complexity of maternal food

168   processing actions predicted this close peering behavior, especially when the food

169   source was a rare one. Peering was typically followed by a juvenile' actions on the same

170   target items in the hour following. In parallel fashion, peering at maternal nest building

171   was recorded over the peak acquisition period for nest building skill, and such peering

172   was followed by a rise in nest building attempts in the subsequent hour. van Noordwijk

173   et al. (2009) also observed youngsters beginning to perform nest-making actions while

174   their mother made her nest, long before the youngster could make its own nest. As

175   authors of these studies concluded, all the quantified observations logged are those

176   predicted by the hypothesis that observational learning pervades a young orangutan's

177   construction of its foraging preferences, food processing and other skills, including nest

178   building.

179   Primate studies that investigate social learning in this way across a breadth of

180   foraging and nesting activities appear to remain rare. However in chimpanzees, in which

181   infants' early experiences are more maternally focused than one might expect from

182   chimpanzees' general sociability (Inoue-Nakamura and Matsuzawa 1997), a study of

183   one specific form of tool use has been telling. Young female chimpanzees spend

184   significantly longer periods observing the termite fishing of their mother than do their

185   male siblings, and these females go on to master the requisite techniques as much as a

186   year earlier than their male peers (Lonsdorf et al., 2004; Lonsdorf 2006). This difference

187   is likely to be of functional significance, since when females reach adulthood, tool-

188   assisted insectivory plays a more important role in their diet than for males, who gain

189   more animal protein from hunting other mammalian prey (McGrew 1979). As in the

190   orangutan analyses these are correlational findings, so the conclusion that most

191   researchers draw, that they indicate social learning, needs to be tempered by the

192   possibility of a genetic mother-offspring link, such as through biases in manipulative

193   propensities. However the finding of an even higher tighter of mother-daughter

194   matching of the length to which stem tools are inserted into termite mounds (a fidelity

195   tellingly not found for the male offspring that have displayed less peering at the

196   termiting process) are harder to reconcile with an effect of genetic inheritance (Lonsdorf

197   et al. 2004). A now very large corpus of experimental and other studies demonstrate a

198   motivation and a capacity for social learning in young apes consistent with these results

199   from the wild (reviewed in Whiten 2017b, c). Matsuzawa (2008), in a graphic phrase,

200 described such acquisition of skills in chimpanzees as a system of 'master and

201 apprentice'. In monkeys living in the wild, selective attention by juveniles has been

202 documented in some detail in white faced capuchins and as in the orangutan studies,

203 found to be focused on relatively rare, large and difficult to process foods (Perry et al.

204 2006, 2017). Moreover in monkeys, the proposed causal role of social learning has

205 begun to be more directly and rigorously tested by field experiments. van de Waal et al.

206 (2013) studied wild vervet monkeys in several groups that once a month were

207 provisioned with a box of maize corn in order to reveal monkeys' ranks and alliance

208 dynamics. For the social learning experiments, the corn was divided into two boxes

209 presented side by side and died either pink or blue, with one color of corn having an

210 additive that made it too bitter to eat in two of the four groups studied, and the other

211 color so treated in two other groups. It took three trials at monthly intervals for the

212 monkeys to learn to avoid the locally unpalatable color. This was done around the birth

213 season so that the new crop of suckling infants were not yet feeding on such solid food

214 so did not test it. After a four-month fallow period allowing infants to mature, the same

215 pink and blue colored corn options were presented again but now with no additive, so it

216 could be tested whether infants who were now starting to eat solid food learned what to

217 eat by trial and error exploration, or were instead biased by maternal preferences. The

218 answer resoundingly confirmed the latter, with 26 of 27 infants starting to take the color

219 preferred in their group. The mother of the other infant was of very low rank, so fed on

220 the alternative food box while higher ranked animals continued with their now long-

221 standing preference, and this infant preferentially took corn of the same color as its

222 mother. Accordingly, 27 of the 27 infants ate the option their mothers ate, even though

223 both colors of corn were now equally palatable.

224   In another experiment, groups of wild vervet monkeys were provisioned with sand-

225 covered grapes (van de Waal et al. 2014). Mothers adopted one of four different

226 techniques to clean them (such as rubbing the grapes in their hands, or rubbing them on

227 the ground) and infants showed a significant matching to the technique displayed by

228 their mother. An earlier report showed that such differences are correlated across

229 matrilines (van de Waal et al. 2012), suggesting that the preferred techniques tend to

230 pass down vertically along these kin lines.

231   A parallel study concerning a very different behavior may reflect very similar social

232   learning in Japanese macaques. Tanaka (1995) conducted fine-grained analyses of video

233   records of the precise way in which mothers removed the eggs of lice from body hair

234   during grooming. Groomers need to free the egg and its ring of cement so that it can be

235   slid up and off a hair and this was done using four different kinds of manipulative

236   configuration, such as using a finger nail to initially scrape the egg loose before sliding

237   it up a hair, or using a 'thumb-jig' to free it before removal. Echoing the vervet results,

238   these styles were found to characterize whole matrilines. Again it might be suspected

239   that genetic inheritance could explain these findings, but evidence against this is that

240   from time to time, the preferred technique changed. In one such case studied in detail, a

241   matriarch was observed to change her technique and her daughters and granddaughters

242   soon followed her in this switch, indicating a social learning effect (Tanaka 1998).

243   Tanaka suggests that such changes imply imitative learning of the actions involved. We

244   postpone to below any in-depth consideration of the psychological processes involved

245   in the social learning of these young primates.

246   Some primates, most significantly callitrichids, deviate from the above picture of an

247   initially primarily maternal context for social learning. In common marmosets, for

248   example, the father typically begins to carry the normally twin infants from birth and

249   later starts to share food with them, whilst the mother is more limited to the necessarily

250   high burden of lactation for these twins. Other individuals in the group, who are

251   reproductively inhibited, may also care for the infants in what is described as a

252   cooperative breeding system (Schiel and Souto 2017). The corresponding context for

253   early social learning has been examined through complementary observational studies

254   in the wild and experimental investigations in captivity. In the wild, Schiel et al. (2006)

255   found that observation of adults or subadults foraging (which principally involves

256   locating, catching and consuming invertebrate prey) peaked in 3-4-month- old infants,

257   occurring in close to 50% of all ten-minute observation bouts. Half these cases resulted

258   in 'model-dependent foraging' in which infants responded within ten seconds of

259   watching a model. This took one of three main forms, involving either manipulating the

260   same object within 5 seconds, foraging closer together, or approaching and acting

261   synchronously, as in feeding on the same food source. Older juveniles of 5-10 months

262   observed others at lower frequencies as they became generally more competent hunters,

263 but when they did attend to others' actions they were still likely to then perform model-
264 dependent foraging.

265   The role of social learning in marmosets was more systematically investigated
266 through experiments in captivity, which contrasted conditions allowing or preventing
267 observation of a model, in naturalistic foraging challenges that involved catching
268 relatively large prey (grasshoppers or crickets) or extracting embedded prey from within
269 covered holes (Dell'mour et al. 2009). Infant observation of adults (their mother, in this
270 study) peaked at a similar age to that earlier recorded by Schiel et al. (2006) in the wild,
271 and these infants were 15 times more likely than non-observers to tackle the problem
272 presented. They also needed significantly fewer trials to achieve mastery. Infants were
273 able to successfully catch and kill insect prey within 5 months so long as they observed
274 their mother hunting the same species. Further below we discuss whether modifications
275 of parental behavior in this context may represent a simple form of teaching.

276   The pattern of early social learning focused on primary caretakers is also apparent
277 in the human primate, from feeding behavior to language acquisition. For example
278 Hewlett and Cavalli-Sforza (1986) conducted in-depth interviews with Aka hunter
279 gatherers in the Central African Republic, asking from whom each of 50 very different
280 skills, ranging from foraging to food sharing to infant care, had been learned.
281 Respondents were reported to offer detailed descriptions of whom they watched
282 performing the skill or the few things the person said to transmit the skill knowledge.
283 From these responses the authors concluded that "unquestionably, parents are the
284 primary contributors" (p. 928), their average contribution being reported as 81% overall,
285 and as much as 89% on average in the case of food-processing skills. These figures
286 might be somewhat inflated in favor of vertical transmission through the self-report
287 methodology (Aunger 2000) but Aunger's own data based on inter-household versus
288 inter-clan cultural similarities in food taboos concurred in describing an initial phase of
289 cultural learning from parents.

290   These results echo a general conclusion with which we close this section, namely
291 that for juvenile non-human primates, it is crucial to have mastered subsistence skills
292 sufficiently well to sustain the independence required by the age of weaning, and the
293 primary caretaker or caretakers, typically the mother, are those providing the main
294 models. In the wild the importance of the latter derives from the fact that what may be a

complex dietary array needs to be selected from a massive range of potential options in the natural environment, that vary much in their nutritional payoffs as well as being noxious or toxic in many cases. Over a year, a community of chimpanzees may exploit over 300 different kinds of food item, including only certain parts of plants such as the peeled pith, the peel itself being toxic; in Lope, Gabon, for example, fruit alone is harvested from 114 different plant species (Inskipp 2005). The preferred items are selected from among hundreds if not thousands of alternative species and parts (flowers, fruits, pith, storage organs). A similar task is faced by gorilla and orangutan infants (Whiten 2017b) and to a greater or lesser extent, all primates.

Given such complexities and dangers in primate feeding niches, trial-and-error learning is likely to be inefficient, if not overtly dangerous given the distribution of poisonous elements adapted to deter consumption, whereas social learning instead taps an existing knowledge base of the community. The importance of social learning may nevertheless vary according to food-type. In a preliminary study of howler monkeys, Whitehead (1986) noted that in the case of mature leaves, that often contain toxins, mothers would often wait until their infant joined them before selecting leaves to eat, and infants always waited for adults to feed first and observed them. By contrast in the case of fruits, that depend on being eaten for seed dispersal, and so are rarely toxic, infants were more likely to initiate their own feeding activities (Whitehead 1986).

The most relevant of the knowledge transmitted may be significantly localized, making learning from a mother familiar with the locality important: for example in comparison to intra-population homogeneity, 60% of the dietary preferences of orangutan populations on either side of a large river were found to be different (Bastian et al. 2010). In a recent review Whiten (2017b) suggested that "years of close apprenticeship to a mother who daily displays her knowledge of such a large but selective diet-set likely provide an important means of achieving an adaptive response to this challenging complexity" (p. 7793). Schuppli and van Schaik (2017) used the metaphor of an iceberg to describe this situation: they suggest we have tended initially to identify only the iceberg's most visible 'tip' of socially learned repertoires, especially salient items like tool use', neglecting the greater of more mundane behavior such as what to eat, where to sleep and what are things and places to beware of. Relatively simple social learning processes, such as stimulus and local enhancement of the relevant

327 items, or overt negative responses to them, may suffice to permit much of this scale of

328 information acquisition, whether in visual, vocal or olfactory modes (see Fig. 1).

329

330 **Widening circles of influence: 'Learning from the best nutcrackers' and other**

331 **functional biases**

332

333 In the case of human childhood, Henrich and Broesch (2011) propose "a two-stage

334 learning model in which individuals first acquire information from their parents … and

335 then later update this information based on information from their preferred models" (p.

336 1140). These authors provide a range of lines of evidence supporting this basic model

337 from a field study in small-scale Fijian villages, where in the second stage proposed

338 above, individuals begin to obtain information from those judged better models than

339 their parents for specialist activities such as fishing, growing yams or medicine. This

340 basic two-phase model maps to what we proposed earlier in this paper for non-human

341 primates: initial learning from primary caregivers, typically the mother (as reviewed in

342 the section above), followed by a progressively widening circle of learning from others

343 (Fig. 1). Experimental evidence consistent with a developmental shift from an initial

344 preference of children to learn from parents to models with alternative expertise has

345 come from controlled studies of both acquisition of manipulative expertise (Lucas et al.

346 2017) and trust in verbal informants (Harris and Corriveau 2011). In non-human

347 primates, the quantitative study of young orangutans' peering behavior mentioned

348 earlier (Schuppli et al. 2016) showed that by about age five, close to weaning, peering at

349 the mother tipped below 50% and became focused more towards others from whom

350 there may yet be something new to learn.

351   Henrich and Broesch (2011) predict the second of the two broad phases to be

352 selective, and they propose and provide evidence from their Fiji studies for a suite of

353 such learning biases, all of which are argued to achieve adaptive outcomes.

354 Emphasizing such inferred functionality, these biases have been referred to in

355 comparative research as 'social learning strategies' (Laland 2004), although labelled

356 elsewhere by other, more neutral terms like 'transmission biases' (Boyd and Richerson

357 1985). Recent years have seen an escalation of published reports about these biases in

358 humans, non-human primates and other species (Rendell et al. 2011; Hoppitt and

359 Laland 2013; Price et al. 2017). As yet only a small proportion of this work has a

360 developmental focus in non-human primates, but sufficient studies are now available for

361 us to address a number of the biases listed by Henrich and Broesch (2011), and we shall

362 add further to these. In what follows, for brevity we describe selectivity in terms of

363 biased 'copying' but we do not necessarily imply high-level processes like imitation by

364 this: if a juvenile is biased to eat what dominant individuals eat, for example, we might

365 express the rule as 'copy high rankers' even though the process may be as simple as

366 stimulus enhancement of a particular food type.

367 Henrich and Broesch's (2011) first and arguably most important bias is

368 "perceived success or knowledge". As an example, they found that in Fiji, believing

369 someone to be among the best spear-fishers increases by a factor of 10 the chances that

370 such experts will be chosen to learn from two years later. For medicinal plant

371 knowledge, the bias rises to a factor of 25. Their finding that perceived success was

372 more influential than inferred knowledge is worth highlighting because non-human

373 primates can in principle judge a potential model's success by direct behavioral

374 observation. A clear primate example is indicated by one paper's title, "Watching the

375 best nutcrackers: what capuchin monkeys know about others' tool-using skills" (Ottoni

376 et al. 2005; see also Coelho et al. 2015; and see Fig. 1). These authors reported that

377 close observation of stone-tool-based nut cracking is prevalent in young capuchins, and

378 that the latter preferentially target the most proficient (and not just the most active)

379 nutcrackers. Nut-cracking adults are tolerant of this close attention and indeed permit

380 scrounging, which occurs in 35% of cases, so this could be the immediate causal

381 explanation for the phenomenon. However the authors highlight that "This simple

382 mechanism could, by itself, optimize the conditions for the social learning of nut-

383 cracking techniques and for the diffusion of tool-aided nut-cracking as a behavioral

384 tradition" (see also Fragaszy et al. 2017). Indeed in marmosets, Caldwell and Whiten

385 (2003) showed through controlled experiments that such scrounging may facilitate

386 social learning of foraging behaviors. Other experimental studies have demonstrated

387 that chimpanzees will discriminate and copy the choices of group-mates who are

388 foraging faster at a resource-rich site than those at a site delivering a lower rate of

389 payoffs (Vale et al. 2014; see also Brosnan et al. 2004, for capuchins) and Barrett et al.

390 (2017) provided evidence of preferential copying of proficient extractive foraging

391   individuals in white-faced capuchins. However none of these three studies specifically

392   targeted juvenile subjects. In an artificial foraging task, Kendal et al. (2014) found that

393   chimpanzees were biased to copy models described as 'knowledgeable' rather than

394   simply discriminating success: these preferred models were those who had been trained

395   to succeed, and the authors speculated that what observing chimpanzees may thus have

396   discriminated was these individuals' confident and purposive approach to the task,

397   given that other potential models were just as successful. However this study also did

398   not target juveniles as observing subjects, and we look forward to more studies on this

399   topic that do so.

400   Henrich and Broesch (2011) also found a bias to learn from older models, model

401   age thus likely acting as an indirect predictor of the best individuals to learn from.

402   Reflecting a similar bias, in field experiments introducing novel nuts to nut-cracking

403   chimpanzees in the wild, Biro et al. (2003) found that juveniles were "highly specific in

404   their selection of conspecifics as models for observation, attending to the nut-cracking

405   activities in the same age group or older, but not younger than themselves." (p. 213).

406   Similarly Barrett et al. (2017), after introducing a new hard-shelled fruit to wild white-

407   faced capuchins, reported a similar bias to observe models older than oneself.

408   A bias to prefer one sex of model over the other was also investigated by

409   Henrich and Broesch (2011), given the division of labor common in Fijian societies. It

410   was found that all subjects were biased to prefer males as models in relation to fishing

411   and yam cultivation, whereas female models were preferred for medicinal expertise.

412   One area where one might expect related biases in primates is when young male

413   primates may need to learn male-related skills that they cannot learn from their mother.

414   In one such example, wild male tufted capuchin monkeys were found to eat more

415   animal foods and forage more for invertebrates along large branches, while females ate

416   more fruits and fed more on leaves and bamboo microhabitats (Agostini and

417   Visalberghi 2005). Correspondingly, juvenile males were found to progressively spend

418   more time with male adults, focusing their food-related attention on them and

419   eventually adopting the typical male array of foraging preferences. In similar fashion

420   but in a different study, only male capuchins acquired stick-probe use, with young

421   males preferentially observing older male experts (Falotico and Ottoni 2014). Mörchen

422   et al. (2017) confirmed the earlier observation of Schuppli et al. (2016) that young

423 orangutans showed a clear dependence on peering at their mother's activities, whereas

424 as they developed, older individuals showed a preference for watching immigrant

425 unflanged (not fully mature) adult males' activities, especially in the nesting and social

426 context. The authors speculate that unflanged males may thus act as cultural vectors,

427 facilitating the transfer of traditions between orangutan populations.

428 In some cases the functional reasons for an attentional bias to one sex may not

429 arise from diet divergence so much as local expertise. In experimental tests of learning

430 to open an artificial fruit by wild vervet monkeys, van de Waal et al. (2010) found there

431 was evidence for social learning only when the model was an adult female. This may

432 make functional sense insofar as females are permanently resident in their ranges while

433 males disperse, so females are likely to be the local ecological experts to preferentially

434 learn from. However this study did not focus on juvenile observers of these female

435 models.

436 A final bias not considered by Henrich and Broesch (2011) (perhaps surprisingly

437 given the many theoretical and modelling studies of Henrich on this topic) is conformity

438 – copying a majority of one's group. Perry (2009) painstakingly logged the frequencies

439 of young white-faced capuchins watching either of two different ways of processing

440 Luehea fruits (pounding versus scrubbing) over their first five years, starting with

441 mothers and extending to others, and found that individuals tended to adopt whichever

442 technique they had witnessed occurring with the greatest frequency overall.

443 All of the above biases are conceptualized as preferences of the learner.

444 However, whom a growing individual may learn from will also be constrained by the

445 tolerance for close proximity by the potential model. This varies between species (van

446 Schaik et al. 1999; van Schaik 2003), and also in relation to intra-specific learner-model

447 pairings, graphically illustrated by Russon's (2003) tabulation of over 50 such potential

448 permutations of age-sex classes in orangutans. Both inter-specific and intra-specific

449 variations may shape constraints on, and opportunities for, social learning.

450

451 **A life-long ontogenetic perspective: social learning at the time of dispersal**

452

453 In the above we proposed two initial phases in the ontogeny of primate social learning:

454 a first focused on the primary caretaker, in most species the mother, and a second

455   characterized by progressive learning from a widening social circle in an individual's

456   group. Here we address a third phase that may occur on dispersal from one's natal

457   group, typically an activity that involves males in some species and females in others,

458   avoiding inbreeding. On dispersal an individual will experience a new physical territory

459   and a new social context. Each of these will likely bear some resemblance to the natal

460   array, but may differ in others, and will certainly do so in important details, all of which

461   potentially creates a significant further phase in which social learning from residents

462   may be beneficial. For example the migrant individual will initially know nothing about

463   where important foraging, drinking and sleeping sites are, and the foraging spectrum

464   may even include new food types and associated foraging techniques (Russon 2003).

465   On the social side there may be much to be learned about local social dynamics, as for

466   example whom to respect for their high rank. Alternatively, a migrating individual may

467   be the possessor of skills not yet present in their new group, so in this case it is residents

468   who may learn from the immigrant, who acts as a tradition-bearer from its natal culture.

469   In the course of the experiment described earlier that used trained group preferences

470   for eating pink or blue corn to test for social learning in infancy, as many as ten male

471   vervet monkeys happened to conduct their dispersal so they moved from a group that

472   mostly ate one color of corn to one that habitually preferred the other color (van de

473   Waal et al. 2013). With a surprising degree of alacrity, all but one of the ten adopted the

474   local preference as soon as they were not outranked at the food source and were free to

475   decide which color to eat (see Fig. 1), a switch also found in avian cultural diffusion

476   experiments where birds similarly dispersed between ranges in which different foraging

477   behaviors had been experimentally created (Aplin et al. 2015). A similar switch to

478   behavior matching that of residents has been described in chimpanzees living in

479   neighboring ranges of the Tai Forest where details of their nut-cracking techniques

480   differ (Luncz et al. 2012). Females transfer between these communities, yet come to

481   behave as do the residents, which in one community involves a year round preference

482   for stone hammers that occurs only seasonally in two others (Luncz and Boesch 2014;

483   Luncz et al. 2015). Similarly, a female chimpanzee migrating to a neighboring

484   community displaying a different style of hand-clasp grooming tended to conform to the

485   new local habit (Nakamura and Uehara 2004)

486   All these cases appear to reflect a disposition to abandon existing personal

487   preferences or behaviors and instead conform to the new local norms. One possible

488   functional explanation is that such a disposition is adaptive in a context of uncertainty

489   about what are the optimal local foraging behaviors to utilize, a good guide to which is

490   offered by the existing residents. A second and quite different adaptive explanation is

491   that by matching the behavior of residents, an incomer may be better accepted into their

492   new group (and social affiliation with those who copy one's behavior has been

493   experimentally demonstrated in macaques by Paukner et al. 2009). At present it seems

494   not possible to clearly distinguish between these two explanations, but in the case of the

495   vervet monkeys, further ongoing tests in overlap ranges that males would already be

496   familiar with may show whether the first, ecological explanation can be discounted if

497   conformity occurs in such regions.

498   Conformity in social behavior is less likely to be consistent with an ecological

499   explanation in any case. Evidence for one such adjustment came in a study of wild

500   baboons in which stealing of infected human food by the most dominant males led to

501   their death (from TB), engendering low levels of aggression in the group. Sapolsky and

502   Share (2004) presented evidence that in later years, as new males entered the group, the

503   peaceful tenor was maintained and hence described as a 'pacific culture' adopted by the

504   immigrants.

505   Cases of the alternative scenario in which instead, immigrant behavior prevails and

506   is adopted by residents appear rare. A case where the inference that this must have

507   happened in the past is offered by nut-cracking in chimpanzees. This occurs only in an

508   area spanning about 500 Km in West Africa and not elsewhere in the entire range. It has

509   been identified in at least eight communities across that Western region (Carvalho and

510   McGrew 2010). Presumably it must have spread through the dispersal of mainly female

511   culture-bearers. When Biro et al. (2003) introduced a new nut species into one of these

512   communities, the nuts were cracked only by a chimpanzee who had migrated from a

513   region where these nuts were already known and cracked. Her practice was

514   progressively adopted by other members of her adopted community, although this

515   process took several years to play out. In one case the technique of ant-fishing spread in

516   a chimpanzee community in which it had not been seen over decades of prior study,

517   following the immigration of a female from a community in which the behavior was

518   habitual (O'Malley et al. 2012).

519

520   **Socio-cognitive transmission processes in primate ontogeny**

521

522   The principal focus of the present review is on the role and scope of social learning in

523   the behavioral ecology of developing primates, irrespective of the underlying

524   mechanisms. However, just what a juvenile primate can acquire by observation, given

525   the particular social learning capacities at its disposal, will constrain its adaptive

526   flexibility. A primate that can copy adults' foraging or tool-use skills through a process

527   such as imitation is in a different adaptive situation compared to one that cannot, and is

528   instead restricted only to such simpler processes as stimulus enhancement, that focus its

529   attention on relevant entities such as the optimal objects to feed on. Accordingly, we

530   here offer an overview of some core relevant findings. Table 1 lists some of the

531   principal psychological processes underlying primate social learning, investigations of

532   which have been reviewed in recent years by Whiten (2012, 2017) and Galef and

533   Whiten (2017).

534   As those reviews confirm, research on primate social learning, which now spans

535   over a century of work, has generated a voluminous literature. This includes a large

536   proportion of laboratory-based studies because these are best able to implement the

537   necessary control and individual testing conditions. For varied and often practical

538   reasons such as subject availability, infants and juveniles figure relatively infrequently

539   as subjects, despite the evidence reviewed above that it is in juvenile phases of the life

540   history where social learning is likely to be particularly prevalent. There are also

541   marked species biases, with a large preponderance of research on chimpanzees, often

542   making comparisons with social learning in our own hyper-cultural species (Galef and

543   Whiten 2017; Whiten 2017c). These biases come together in the fact that a suite of

544   influential experimental studies has documented cultural transmission of alternative

545   tool-use and other techniques spreading within and even between chimpanzee

546   communities, but these have been largely composed of adults (reviewed in Whiten

547   2011).

548   The now extensive corpus of experimental studies dissecting social learning

549   processes have principally focused on whether imitation, defined as copying the form of

550   another's actions (Whiten and Ham 1992) and assumed to be the most complex and/or

551   specialized process, is in operation, or some simpler alternative. The latter include

552   stimulus enhancement and local enhancement, which draw the attention of the learner to

553   particular objects or locations respectively, and emulation, in which an observer learns

554   about the environmental results of actions rather than the form of the actions themselves

555   Table 1). Perhaps bizarrely, relatively little experimental work has accordingly focused

556   specifically on the supposed simpler processes, despite the real possibility that they may

557   play the major role in much of juvenile primates' social learning in the wild. The

558   findings we reviewed indicating extensive social learning about what species, and

559   which parts of them, to eat, require only a role for stimulus enhancement, while local

560   enhancement could engineer learning about beneficial foraging locations, sleeping sites

561   and associated travel routes. Much circumstantial, correlational evidence is consistent

562   with this as reviewed in earlier sections of this paper, yet the only field experiment

563   directly testing such effects we are aware of is our own, in which as described earlier,

564   mothers were trained to prefer either pink or blue corn, a preference their infants did

565   indeed follow faithfully when they began to sample these foods (van de Waal et al.

566   2013). Scrounging food scraps from the mother or others may help funnel infants' focus

567   on the selectivity of experienced models, as shown by experimental tests (Caldwell and

568   Whiten 2003). However, given that several studies with captive primates have reported

569   a lack of such discrimination (Fragaszy et al. 1997), more tests in the wild are needed to

570   clarify whether such apparently conflicting findings reflect the effects of captive rearing

571   (discussed further by Perry and Ordoñez Jiménez 2006).

572   The enhancement effects outlined above have a positive valence (i.e. are positively

573   valued by the animal concerned), which may also apply to domains other than foraging,

574   drinking and sleeping, such as in mate choice copying, for which there is evidence in

575   fish (Dugatkin 1996). However the corresponding experiments needed to test such

576   effects are rather intractable in primates. Other enhancement effects may have negative

577   valence (i.e. be actively avoided by the animal). The most obvious functional example

578   and perhaps the most critical one is avoidance of predators, where laboratory

579   experiments have shown juvenile macaques quickly developing fear responses to

580 objects that their mother showed fear of (Mineka and Cook 1998; see Russell et al.

581 1997, for chimpanzees). In an apparent parallel in the vocal domain, Cheney and

582 Seyfarth (1990) described how juvenile vervet monkeys, although apparently having

583 innate biases to use different alarm calls for aerial and terrestrial predators, nevertheless

584 showed a progressive convergence on the specific targets eliciting alarm calls by

585 experienced group members, initially calling when sighting (harmless) vultures but later

586 ignoring them, whereas the response to martial eagles, with which adult calls are

587 associated because they are the true danger, became the strongest, suggesting learning

588 from these experienced adults. Equivalents to such negative valence in non-predator

589 contexts such as foraging appear less prevalent. One potential example comes from

590 observations on a mother chimpanzee responding to her infant reaching for leaves of a

591 non-food tree: "her mother, FT, took PN's hand and moved it away from the leaves. As

592 PN continued … FT took the leaves from PN's hand, plucked all the leaves within her

593 arm's reach and dropped them to the ground" (Haraiwa-Hasegawa 1990, p. 280). Other

594 mothers behaved similarly and they "prohibited … infants only from feeding on the

595 individual trees that they themselves never fed on".

596   Turning to focus on the role of imitation in primate development, it is generally

597 assumed that this is the most cognitively complex of the social learning processes. This

598 is because imitation requires the transformation of forms of action by others that are

599 perceived in some sensory modality (the visual modality being most analyzed, but

600 imitation can also refer to vocal copying) into appropriately matching motor outputs by

601 oneself (Whiten and Ham 1992). Imitation is also often assumed to permit the highest

602 fidelity of transmission of action patterns, thus providing strong support to the spread

603 and maintenance of cultural traditions, and in the view of numerous authors, key in the

604 emergence of human cumulative culture (Tomasello et al. 1993; Henrich and Tennie

605 2017). Both cumulative culture and imitation itself have been argued to be limited only

606 to our own species (Tennie et al. 2009). Such conclusions assert that non-human

607 primates' most complex social learning is limited to emulation, characterized by

608 learning only about the environmental results of actions rather than the actions

609 themselves.

610   However the imitation-emulation dichotomy is not so clear as at first sight. It is not

611 straightforward where the boundaries of 'actions' that may be copied ('imitation') lie.

612   One criterion some authors adopt is that only *bodily* copying counts as imitation (e.g.

613   Tennie et al. 2012). But when a tool is used, it becomes effectively an extension to the

614   body, so is copying the form of a tool's movement, as in for example poking versus

615   levering, emulation or imitation? Perhaps copying such movements may have similar

616   cognitive requirements to copying the form of particular body movements, and have

617   similar implications for the faithful transmission of cultural patterns. In such contexts,

618   both imitation and emulation may be involved – and beneficial in copying the 'gestalt'

619   of the bodily and tool movements and their effects. Similar considerations can be

620   extended to the form of the changes a tool or a hand may effect on an object such as a

621   fruit, so we may envisage a continuum in the causal sequence of bodily and

622   environmental happenings that may be copied, possibly with associated tool-based

623   happenings in between.

624   Just what parts of this causal cascade of bodily and external happenings are copied

625   (and in particular whether details of bodily movements are imitated) may not

626   necessarily constrain the long term life of a tradition. For example we have

627   archaeological evidence that tool-based nut-cracking by chimpanzees has been

628   transmitted for over 4,000 years (Mercader et al. 2007), a long period of faithful

629   transmission compared to most contemporary human traditions one can think of, and we

630   also have experimental evidence that the transmission of this skill to juveniles rests on

631   social learning (Marshall-Pescini and Whiten 2008; Whiten 2015). High fidelity motor

632   matching may not be essential to such cases (see also Fragaszy and Visalberghi, 2001):

633   so long as a rough copy of the hammering action is refined through extensive cycles of

634   practice and observation, and delivers important nutritional payoffs, nut-cracking may

635   well be sustained with adequate fidelity down the ages, as every generation of juveniles

636   copies what they see existing experts do, and confirm it delivers great rewards.

637   Nevertheless, ghost experiments in which environmental effects are made to occur

638   with no agent visible indicate that seeing another individual *do actions* facilitates

639   learning of their consequences in the more elaborate cases (Hopper et al. 2007, 2008,

640   2015). Direct evidence that apes can imitate bodily actions, even if with lower fidelity

641   than children, comes from 'Do-as-I-do' experiments in which the subject is taught to try

642   to replicate a training set of bodily actions when requested, then tested on a novel

643   battery of manual, facial and gross bodily movements. These were first reported for a

644   young home-reared chimpanzee by Hayes and Hayes (1952), then later replicated with

645   non-enculturated 'lab' chimpanzees by Custance et al. (1995) and Pope et al. (2018) as

646   well as with an enculturated adult orangutan by Call (2003). Evidence that chimpanzees

647   observing others are cognitively encoding what they see in terms of actions comes from

648   a case where in one juvenile this 'spilled over' the normal inhibition that occurs while

649   watching an act that may later be imitated. This youngster instead acted out the nut

650   cracking actions while watching the older chimpanzee perform, sometimes even in

651   approximate synchrony (Marshall-Pescini and Whiten 2008; Führman et al. 2014). The

652   youngster had no hammer or nut, so this could not be emulation.

653   Similarly, young enculturated chimpanzees and orangutans observed a model and,

654   after a ten minute delay, they often replicated the actions the model had performed

655   (Bering et al. 2000; Bjorklund et al. 2000). These studies tested copying of a large

656   range of actions on many different objects, demonstrating matching in such witnessed

657   acts as holding a drill in one hand and turning the crank to make it drill, or putting a nail

658   in a form board and using a hammer to hammer it.

659   Such copying can be selective in ways that may be regarded as rational. Horner and

660   Whiten (2005) showed that young chimpanzees tended to copy all parts of an action

661   sequence used to extract food from an opaque artificial fruit, but when some parts of the

662   action sequence could be seen to be ineffective in a transparent version, these were

663   likely to be omitted from the apes' own efforts. Children, by contrast, tended to copy

664   these, a response later labelled 'over-imitation' (Lyons et al. 2007), which has spawned

665   a now-substantial research literature in developmental psychology, as well as two

666   replications of the ape results (Nielsen and Susianto 2010; Clay and Tennie 2018).

667   Evidence of bodily imitation in primates is not restricted to apes, although to our

668   knowledge, experimental tests with monkeys have not included juvenile subjects, as the

669   ape research has. Voelkl and Huber (2000) showed that compared to a sample of

670   marmosets that typically used their hands to open an artificial food canister, those who

671   witnessed a model use her mouth were more likely to apply that method. Since this had

672   the same effects on the canister, the difference could not be explained by emulation but

673   rather bodily imitation, even if at a crude level of manual versus oral manipulation.

674   Similar evidence for imitation in birds using either their beaks or feet to produce the

675   same environmental effects have been demonstrated in more than one species of bird

676 (Zentall 2004) and the same mouth/hand copying was replicated for wild-born vervet

677 monkeys in a sanctuary in South Africa by van de Waal and Whiten (2012), followed

678 by spread of the preference for different techniques within models' respective groups.

679   In a very different experimental approach, de Waal and Johanowicz (1993)

680 managed to cross-foster two species of macaque, only one of which naturally displays a

681 strong disposition to display reconciliatory responses after aggression, and found that

682 such behavior became more common in the monkeys reared with the conciliatory

683 species. It is difficult to see how this could come about by a process that fits the

684 conception of emulation, suggesting it rested on copying the behavioral dispositions of

685 the adult society the youngsters were cross-fostered in.

686   The transmission of a variety of other behavior patterns in monkeys appears

687 difficult to explain other than by imitative copying. A striking example is what Perry et

688 al. (2013) described as social conventions, in which bizarre habits of pushing fingers

689 into the mouth, nostrils and even eye sockets of close companions arose, diffused in

690 certain groups and later faded, in white-faced capuchins, which seems difficult to

691 acquire other than by imitatively mirroring what another monkey does to oneself. In a

692 very different example, Leca et al. (2007) identified as many as 39 different forms of

693 the strange 'stone-handling' behaviors of Japanese macaques, different arrays of which

694 were exhibited in different groups, again suggesting copying of the local behavior

695 patterns.

696   Perhaps surprisingly, emulation behavior has been little tested explicitly, instead

697 tending to be the default explanation offered for social transmission where there is little

698 or no evidence of imitative matching. An interesting exception is an experiment by

699 Tennie et al. (2011), who showed (adult) chimpanzees how to pour water from a bottle

700 into a tube, so that a peanut inside rose high enough to be extracted. Nearly a third of

701 the subjects, who were then presented with a dry tube and peanut but no bottle, took

702 water into their mouths from their dispenser and spat it into the tube to create the same

703 effect, demonstrating emulation in the original sense suggested by Wood (1989) and

704 Tomasello (1990).

705   Teaching, defined functionally rather than intentionally as any behavior performed

706 at a cost to the teacher that benefits the development of competence in the pupil, has

707 been increasingly documented in a variety of species in recent years (Hoppitt et al.

708   2008; Thornton and Raihani 2008). In mammals, this is often in predatory species

709   where the young need to make a big leap from nutrition based on maternal suckling to

710   catching and dispatching elusive prey. We suggest that the best evidence for teaching in

711   primates fits this context, as illustrated in the behavior of callitrichid adults that on

712   finding their typical invertebrate prey such as insects, emit vocalizations that attract the

713   young but themselves desist from prey capture, so 'scaffolding' the youngster's initial

714   attempts at predation (Rapaport and Ruiz-Miranda 2002; Rapaport and Brown 2008;

715   Dell'mour et al. 2009). Perhaps the closest to this in other primates is displayed in the

716   tolerance of mothers to allow young to take their tools and food targets, such as in

717   chimpanzee nut cracking (Boesch 2012) and termite fishing (Musgrave et al. 2016). We

718   judge that the suggestion of Hoppitt et al. (2008) that teaching is not as elaborate in

719   chimpanzees as one might expect from the sophistication of some aspects of their social

720   cognition appeals to the functional context: unlike for predatory species, the transition

721   from suckling to foraging on items like fruits can be an easier and more direct one, that

722   can be adequately achieved by observational learning alone.

723

724   **The roles of juveniles in primate culture: social learning, play, innovation and**

725   **practice**

726

727   In a remarkably prescient early paper, "The nature and uses of immaturity", Bruner

728   (1972) suggested that understanding the nature of primate development and in particular

729   the 'evolution of educability' (p. 688) requires analysis of both social learning and play,

730   the latter occupying so much of a juvenile primate's life. Despite decades of research

731   (Bruner et al. 1976; Fagen 1981; Bateson and Martin 2013), the function or functions of

732   play have yet to be compellingly demonstrated, perhaps in large part because play

733   cannot be easily experimentally manipulated, limiting our ability to clearly establish

734   causation with respect to its proposed benefits. Nevertheless, there is something of a

735   consensus amongst the authors cited above that play provides a form of uniquely

736   flexible (rather than rote) practice. Fagen (1976) proposed an insightful analogy with

737   what engineers can discover by running programs to guide a model aeroplane's extreme

738   ('playful') explorations of its actions in a wind tunnel, feedback from which can be

739   utilized to make the program more sophisticated in its response to future challenges that

740 cannot be predicted in all detail in advance. Accordingly Fagen described play as

741 'optimal generic learning by experimentation' (p. 99). The essence of Bruner's linkage

742 of observational learning to this conception of play was elaborated upon by Whiten

743 (2015) in a graphic designed to model the ontogeny of nut-cracking behavior and

744 similar difficult skills in chimpanzees (Fig. 2). Here, following a bout of observational

745 learning, the juvenile applies what it has learned in playful exploration and practice.

746 Then, with the benefits of such actions and the feedback they generate available, the

747 youngster returns to observe an adult model again, now being able to extract more

748 applicable information than before. This cycle continues until the skill is effective and

749 the benefits of further observation attenuate. A further 'twist' to this helical model is

750 suggested by Russon's (2003) point that changes in age-related competencies (and

751 strength) can change an individual's approach to a task such as complex manipulative or

752 tool-based foraging problems, so these need to be 're-solved' in different ways through

753 development, potentially with the aid of further observational learning from skilled

754 individuals.

755

756 *** please insert Figure 2 about here ***

757

758   Apart from its potential role in individual ontogeny, the innovative aspect of play

759 suggests a potential role for juveniles and their playful explorations in the population-

760 level phenomena of cultural evolution, because innovation is necessary for evolutionary

761 change. Such effects might in principle extend to cumulative culture, in which

762 innovation builds on earlier inventions that have already been incorporated into current

763 traditions. Early and famous examples are due to Imo, the juvenile female Japanese

764 macaque who first invented sweet-potato washing and later wheat grain sluicing, that

765 led to some of the first reports of primate 'proto-cultures' (Hirata et al. 2001, for a

766 review). Imo's inventions first spread to her juvenile peers and eventually to adult

767 females, thence being transmitted vertically down to offspring, in line with the picture

768 we presented in the first section of this review.

769   Innovation, whether playful or not, has been subjected to little systematic study in

770 the field, perhaps in part due to difficulties in defining and measuring it. However a

771 major and rigorous onslaught on the topic has recently been completed by Perry and her

772 colleagues, in a 10-year study of 10 groups of white faced capuchins, extending to the

773 lives of 234 individuals (Perry et al. 2017). Innovations were defined and recorded in

774 the latter five years of the project as those behaviors that no researcher had seen in the

775 group in the prior five years, with each of these two periods yielding over 35,000 hours

776 of observation. In total 187 such innovations were identified across the domains of

777 foraging, social, investigative and self-directed behaviors. The majority of these were

778 never taken up by others, with no more than 22% being later socially transmitted. For

779 example, using the tail tip to sponge water out of tree holes arose in four groups over

780 the whole ten year period but only spread socially in one of them. That a majority of

781 novel behaviors are not necessarily picked up by others echoes the results of a

782 retrospective analysis of records of innovation in Mahale chimpanzees, reporting that

783 only 11 of 32 behaviors never seen in the first 15 years of a 40-year study spread

784 significantly among others (Nishida et al. 2009). These authors conclude that "It

785 appears to be difficult for a new behavioral pattern to propagate from a single newcomer

786 to many members of a society … In contrast, it seems to be easy for a newcomer to

787 acquire an established pattern, as was seen for subadult female immigrants who quickly

788 became habituated to human observers after immigration" (p. 34: see Samuni et al.

789 (2014) for documentation of the latter effect in a different chimpanzee community).

790 Nishida et al. (2009) comments that ''from many to single, that is, socialization" may be

791 a relatively easy process, by contrast with the launching and spread of a new innovation.

792 As we remarked in reporting our pink-and-blue corn experiment, this would be the

793 consequence of a social learning bias to copy the majority in one's community, and

794 perhaps explains why social learning appeared potent in our colored corn experiment,

795 compared to other field experiments that instead seeded new foraging techniques in only

796 single initial models.

797 　　Perry et al. (2017) found that juveniles were responsible for a majority of

798 innovations overall, spanning domains of foraging, investigation and self-directed

799 behavior, whereas adults generated more innovations in the social domain, such as the

800 'bond-testing' behaviors involving mutual insertion of fingers into each others' nostrils

801 and eye-sockets. The authors argue that these biases are functional, as juveniles'

802 learning and exploration is principally focused on foraging and other survival skills,

803 whereas in adulthood social dynamics, including bond testing through changing social

804 customs, become more critical for reproductive success. The quantitative results of this

805 study thus appear to confirm the early speculations of Bruner (1972) outlined above,

806 that the playful and exploratory mode of primate juvenility plays a significant role in

807 innovation, interacting with processes of social learning both at the individual level

808 ('the helical curriculum': Fig. 2) and transmission at the broader cultural level (as

809 innovations are necessary to cultural change).

810 These results do differ, however, from a large scale survey of the primate literature

811 undertaken earlier by Reader and Laland (2001). Scoring the literature up to this date

812 for records of behavior described as novel or innovative, these authors logged 533

813 instances, 45% of which concerned foraging. The significant finding for our present

814 discussion is that they reported a majority of innovations by adults rather than juveniles,

815 which as the authors noted, "runs counter to contemporary thinking" (p. 801). However

816 this survey had to depend on what primate researchers each deemed 'innovative' or

817 'novel', with little hope of standardizing this. The contrast with the rigorous and

818 prospective collection of relevant data in the study of Perry et al. (2017) could hardly

819 contrast more. More data of this kind will be needed to clarify the significance of

820 juveniles' innovations.

821

822 **Summary and Conclusions**

823

824 As suggested in our title, there is mounting evidence that social learning typically

825 pervades primates' lifetimes across multiple domains. Of course this is not to argue that

826 individual-level exploration and learning is unimportant: to the contrary, we have

827 emphasized above a continued alternation and integration of what is acquired through

828 social and asocial learning. We find that the three major phases of social learning that

829 we outlined fit many of the findings available for primates including the great apes and

830 a majority of the monkeys, as well as Strepsirrhine primates where relevant data exist.

831 The third phase following dispersion probably occurs in all species, although in each,

832 just those who migrate. By contrast the transition between a first phase of learning from

833 primary attachment figures and a subsequent phase of learning from an expanding array

834 of others is likely to be more graded and vary between and within species, in part

835 modulated by variations in competition and tolerance (van Schaik 2003). For example,

836 the unusually committed role of fathers in callitrichidae was mentioned; and just how

837 the ontogeny of social learning is distributed in many other taxa, such as monogamous

838 gibbons, appears to remain largely undocumented. Accordingly, given the patchiness of

839 the data we have been able to draw together in this review, we propose our overarching

840 three-phase scheme should be regarded as a working heuristic hypothesis, We hope that

841 expressed in these tentative terms, our review will help researchers fill the major gaps

842 that still exist in our knowledge of the ontogeny of primate social learning.

843

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1186

1187   Table 1. Glossary of key social learning concepts
1188
1189   *Conformity:* Adherence to majority behavior overrides personal adherence to an
1190   alternative option (*Conformist bias:* Probability of adopting majority behavior exceeds
1191   proportion of community showing it).
1192   *Cultural transmission:* Diffusion of behavior patterns via social learning from others'
1193   actions or their consequences.
1194   *Culture:* (a) broad sense – equivalent to 'Tradition' below; (b) special sense – a
1195   communal complex of multiple traditions (Whiten and van Schaik 2007).
1196   *Emulation:* An observer replicates the desirable results of another individual's actions
1197   but using a different means to do so.
1198   *Imitation:* An observer copies the form of the actions of another individual.
1199   *Local enhancement:* An observer's attention is drawn to a particular location by the
1200   actions of another individual.
1201   *Social learning:* Learning from others: more specifically, 'learning that is influenced by
1202   observation of, or interaction with, another animal (typically a conspecific) or its
1203   products' (Heyes 1994). Social learning can occur through various specific processes
1204   listed in this table, including emulation, imitation, local and stimulus enhancement, and
1205   teaching (Whiten et al. 2009).
1206   *Stimulus enhancement:* An observer's attention is drawn to a particular object by the
1207   actions of another individual.
1208   *Teaching* (defined functionally): Behavior performed at a cost to the teacher, which
1209   benefits the developmental achievements of a pupil (for extended definition see Caro
1210   and Hauser 1992).
1211   *Tradition:* A behavior pattern shared by members of a community that relies on socially
1212   learned and transmitted information.
1213   *Horizontal transmission:* Cultural transmission within a generation.
1214   *Vertical transmission:* Cultural transmission from parent to offspring.
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1217   Figure captions
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1219   Fig. 1 Three proposed major phases in the ontogeny of social learning in monkeys and
1220   apes. For full explanation, see text
1221
1222   Fig. 2 'Helical curriculum' model of social learning of complex skills. Educationalists
1223   talk of a 'spiral curriculum' in which topics are re-visited at increasingly higher levels -
1224   but representing the developmental time dimension creates a 3D helix rather than a 2D
1225   spiral. At each turn of the helix, a juvenile watches a model and learns from them.
1226   Between such observational episodes is a period of exploration and playful practice, as a
1227   result of which the learner is able to extract additional information in consecutive
1228   observational periods, including more refined aspects of the skill that the youngster
1229   could not assimilate earlier. Corresponding skill levels thence rise progressively,
1230   indicated by levels 1-5. Modified after Whiten (2015, 2017)
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Phase 1. Learning from mother or other primary attachment figure. Baboon infant sniffs novel food mother is eating. Photo: A. Whiten
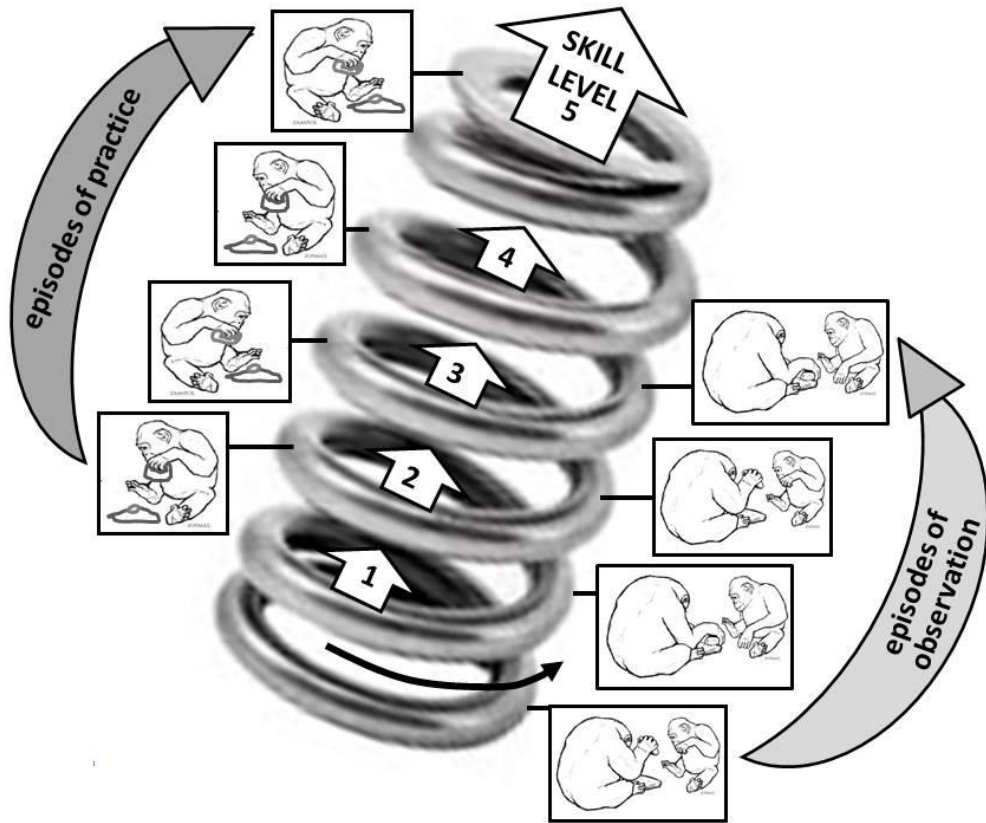
Phase 2. Selective learning in an expanding social world. Juvenile capuchin observes expert adult male nutcracking . Photo: T. Falótico

Phase 3. Learning from residents after migration. Male vervet switches to eat colored corn prefered by new group. Photo: E. van de Waal

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episodes of practice

SKILL LEVEL 5

4

3

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1

episodes of observation

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