Abstract

Researchers investigating the evolutionary roots of human culture have turned to comparing behaviours across nonhuman primate communities, with tool-based foraging in particular receiving much attention. This study examined if natural extractive foraging behaviours other than tool selection differed across nonhuman primate colonies that had the same foods available. Specifically, the behaviours applied to open the hard-shelled fruits of *Strychnos* spp. were examined in three socially separate, semi-wild colonies of chimpanzees (*Pan troglodytes)* that lived under shared ecological conditions at Chimfunshi Wildlife Orphanage, and were comparable in their genetic makeup. The chimpanzees (N=56) consistently applied six techniques to open these fruits. GLMM results revealed differences in the number of combined technique types to open fruits across the colonies. They also showed colony differences in the application of three specific techniques. Two techniques (full biting and fruit cracking) were entirely absent in some colonies. This study provides empirical evidence that natural hard-shelled fruit-opening behaviours are distinct across chimpanzee colonies, differences that most likely have not resulted from ecological and genetic reasons.

Key words: chimpanzee, extractive foraging, hard-shelled fruits, culture, social learning.

26 **Introduction**

27 To augment the understanding of the origins of human culture, scientific research has paid

28 particular attention to wild nonhuman primate communities and their extractive foraging

29 behaviours, such as using tools for cracking nuts or harvesting insects (Whiten et al. 2001;

30 Biro et al. 2003; Schoning, et al. 2008). The traditional approach here has been the method of

31 exclusion where specific behaviours present in one primate community, but absent in others,

32 have led researchers to claim socially learned traditions in nonhuman primates (Whiten et al.

33 2001; Whiten et al. 1999; Schoning, et al. 2008; van Schaik et al. 2003; van Schaik and Knott

34 2011). Critics, however, argue that such reports of population-specific foraging behaviours

35 remain inconclusive because geographically distinct populations are likely to have different

36 food resources and tools available, making it impossible to fully exclude ecological

37 explanations (see Tennie et al. 2009; Gelef 2004; Laland and Janik 2007). While a recent

38 study has reported that chimpanzee communities living in the same area of the Taï Forest in

39 the Ivory Coast selected tools of different materials to open nuts (Luncz et al. 2012), research

40 is still needed to determine whether the actual behaviours underlying natural foraging, other

41 than tool selection, differ across nonhuman primate communities that have the same food

42 available. This study represents an attempt to do so by comparing a range of techniques for

43 opening the hard-shelled fruits of *Strychnos* spp. (commonly called monkey fruit or bush

44 orange) in three socially separate chimpanzee colonies living in a shared environment.

45

46 Experimental studies investigating captive nonhuman primates have provided evidence that

47 techniques used to obtain food from artificial feeding devices can be socially transmitted (e.g.

48 Bonnie et al. 2006; Horner et al. 2006; Dindo et al. 2008). Novel techniques that are seeded

49 into social groups have been found to spread with robust fidelity (Horner et al. 2006; Whiten

50 et al. 2007; Hopper et al. 2011; Dindo et al. 2008; Crast et al. 2010; van de Waal 2013).

51 While such behaviours seem to be socially acquired, they may not be representative of

52 foraging in the wild. Field experiments are a recent development whereby experimental

53 criteria are applied to attempt to control for ecological conditions when studying wild

54 nonhuman primates. Biro et al. (2003) and Gruber et al. (2009) reported socially acquired

55 tool-based foraging techniques in chimpanzee groups for experimentally induced nuts and

56 honey traps, respectively. van de Waal et al. (2010; 2013) and Kendal et al. (2010) found that

57 wild vervet monkeys and lemurs, respectively, showed socially learned solutions to 'two-

58 action' puzzle tasks. While these findings show that neighbouring primate communities can

59 differ in the methods applied to extract the same food, observational studies on semi-free-

60 ranging nonhuman primates are still lacking.

61 An alternative factor often overlooked in social learning research is the impact of group

62 demographics. Nonhuman primates of different age and sex groups may differ in tool use

63 (Inoue-Nakamura and Matsuzawa, 1997; Boesch and Boesch 1984; Lonsdorf 2005; Fessler

64 2002; Gruber, et al. 2010). For example, immature chimpanzees often omit important stages

65 of nut cracking with stones (Inoue-Nakamura and Matsuzawa 1997), and acquisition of

66 expertise is a gradual process of adjusting techniques based on observing adult models

67 (Inoue-Nakamura and Matsuzawa 1997; Lonsdorf et al. 2004; Corp and Byrne 2002; Boesch

68 and Boesch 1984). Furthermore, several reports have documented that female chimpanzees

69 use tools more often and that they forage more efficiently than males (McGrew 1979; Pruetz

70 and Bertolani 2007; Lonsdorf et al. 2004; Gruber et al. 2010). Studies also suggest that

71 primate sex-specific foraging behaviours may both be socially-mediated (van de Waal 2010;

72 Agostini and Visalberghi 2005) and offer evolutionary advantages (McGrew 1979; Pruetz

73 and Bertolani 2007; Fessler 2002). Such findings indicate that group demographics may play

74 an important role in the social-acquisition of foraging behaviours. Therefore, in the current

75 study, group demographics received particular attention.

3

76   Since research on population-specific foraging has focused almost exclusively on tool

77   use (Whiten et al. 2001; Schoning et al. 2008; van Schaik and Knott 2011), a range of

78   naturally challenging foraging tasks have been overlooked. Opening a hard-shelled fruit

79   without a tool, for instance, is of special research interest. It is likely to be a challenging task

80   for primates, as success here depends upon strategies that combine physicality and cognition,

81   in this way sharing features with tool use (Stokes and Byrne 2001). Further, chimpanzee

82   populations from West to East Africa process hard-shelled fruits, as do other wild primates

83   throughout the world (e.g., aye-ayes, sakis, uakaris, capuchins, baboons, orangutans, and

84   bonobos: Koops et al. 2010; Matsumoto-Oda and Kasagula 2000; Lucas et al. 2011; van

85   Lawick-Goodall 1973; Mackinnon 2006; Sterling et al. 1994; Rosenberger and Hartwig

86   2011). This widespread consumption implies that comprehensive analyses of the opening

87   techniques involving hard-shelled fruits can provide a valuable contribution to the literature

88   spanning primate learning strategies alongside social and physical cognition.

89   The present study approach was to provide an overall analysis of the techniques

90   chimpanzees use to open the hard-shelled *Strychnos* fruits and how they utilise these

91   techniques, by comparing age and sex groups across three chimpanzee colonies at

92   Chimfunshi Wildlife Orphanage, Zambia. *Strychnos* fruits are among the most shared fruits

93   between female chimpanzees and their infants at some sites in the wild (Nishida and Turner

94   1996). The current study ruled out potential ecological influences by comparing socially

95   separate colonies with the same specific foods available, living under equal ecological

96   conditions. It is also important to note that the chimpanzee colonies were originally formed of

97   orphans from different places in Africa, housed by arrival date, not (phylo-)geographical

98   background. Based on previous findings suggesting some forms of social learning for

99   foraging (Luncz et al. 2012; Gruber et al. 2009; Horner et al. 2006; Whiten et al. 2007), we

100   hypothesised that chimpanzees of different social colonies would apply different feeding

4

101 behaviours that did not require tools, independent of available resources, group composition

102 and phylogeny.

103

104 **Methods**

105 **Subjects and colonies.** Subjects were 56 chimpanzees at Chimfunshi Wildlife Orphanage

106 (CWO), Zambia: 17 adult and adolescent males, 24 adult and adolescent females, 6 juvenile

107 males (4-8 years of age), and 9 juvenile females (5-8 years of age). They were members of

108 three stable, multimale-multifemale colonies with natural fission-fusion dynamics. Colonies

109 1, 2 and 3 included 27, 18, and 11 subjects, respectively. Table S1 shows the subject

110 representation for age and sex groups per colony, as well as overall colony composition

111 (Colonies 1, 2 and 3 comprised 45-50, 24 and 13-14 chimpanzees, respectively, during the

112 recording periods).

113 The largest colony (Colony 1) and middle-sized colony (Colony 2) lived in 77 and 65

114 hectare (ha) enclosures, respectively. The smallest colony (Colony 3) lived in a 25ha

115 enclosure from August 2010 and in a 2ha enclosure before that. Only one subject, an adult

116 male, was recorded opening fruits (6 fruits) in the 2ha enclosure. The enclosures contained

117 naturally developed fruit groves, grasslands and forests in the miombo woodland. Walls,

118 trees, and fencing meant that the subjects could not observe chimpanzees that lived in the

119 other colonies, at any times.

120 Colony formations took 2-5 years and ended 5-18 years before data collection. Each

121 colony was composed of a mixture of wild-born chimpanzees and chimpanzees born at CWO

122 (see Davila-Ross et al. 2011). The colonies were organised by the arrival dates of the wild-

123 born chimpanzees, not by their (phylo-)geographical background. Thirty-eight of the colony

5

124   chimpanzees were presumably wild-born and brought individually or in pairs to CWO, often

125   from African countries that do not have wild chimpanzee populations. Twenty-four of them

126   (Colony 1: 13 chimpanzees; Colony 2: 6; Colony 3: 5) were brought from countries where

127   wild chimpanzees live (e.g., Tanzania, Uganda, Rwanda). If they were born there, then the

128   subspecies representation for these individuals would be 42-65% for *Pan troglodytes*

129   *schweinfurthii* and 31-42% for *P. t. troglodytes* across the three colonies (Wilson et al. 2008;

130   Tutin et al. 2008). As we do not know with certainty if these chimpanzees were born in these

131   countries, this estimation on subspecies representation was only presented to show that each

132   colony very likely includes a mix of subspecies and that no apparent sign for phylogenetic

133   differences could be found across the colonies.

134   ***Strychnos* fruits, feeding sessions, and data collection.** The fruits from *Strychnos* spp.

135   (Figure S1) weighed approximately 335g (range: 200-460g) and had a diameter of 8.5cm

136   (range: 7.0-9.7cm), based on means calculated for five fruits. The *Strychnos* plants do not

137   naturally grow in the chimpanzee enclosures (nor have they been planted there). Instead, the

138   fruits were provided to the chimpanzees by their keepers. All fruits were bought from local

139   farmers. Fruits were randomly distributed among the colonies, such that all three groups were

140   provided with quantities of fruits proportional to group size, and were overall comparable in

141   size, firmness, colour and ripeness (some ripe and some less ripe). It is, therefore, unlikely

142   that the hard-shelled fruits differed in ways that could have explained differences in feeding

143   behaviours across colonies. These fruits were being given to the chimpanzees of CWO before

144   the present study began, at least since 2005. To the authors' knowledge, no human had ever

145   shown or taught the subjects how to open hard-shelled fruits on any prior occasions.

146   In each of the enclosures, feeding took place within an (approximately) 20 square

147   meter area, close to the enclosure fences which allowed unobstructed viewing from as close

148   as 1-2 meters to the chimpanzees. The feeding areas of Colonies 1 and 2 were roughly 200

6

149 meters from each other, with the miombo woodland separating them, while the feeding area

150 of Colony 3 was about 1.5 kilometres further away. Each feeding area consisted of mainly

151 dried ground, resulting in a hard surface with little grass and sporadic trees. The chimpanzees

152 could, therefore, see their own colony members during feeding.

153   Feeding sessions were video-recorded with the objective of including as many

154 subjects as possible. Recordings were made in 2007 (June-August), and in 2011 (August).

155 Two subjects were video-recorded both as juveniles and as adolescents during the two

156 recording periods. To avoid pseudoreplications, only the adolescent data were included, as

157 this was the age group from which most data were obtained for both subjects. The

158 chimpanzees were fed *Strychnos* fruits 2-7 times a week during the study period. Feeding

159 sessions took place for all colonies between 11:30am and 1:30pm each day, and video

160 recordings were made from just outside the fence at the feeding sites.

161 **Behavioural coding.** A fruit-opening technique was defined as a distinct method applied by

162 a chimpanzee to open a fruit using the mouth, hands and/or feet. Subjects may have used the

163 same technique more than once, as well as combined a range of techniques for each fruit.

164 Repeated as well as individually-shown behaviours were tallied as fruit-opening events. For

165 example, if a subject hit a fruit twice against the ground and then used a specific biting

166 technique once, three fruit-opening events were counted. The study included a total of 939

167 fruit-opening events (Mean = 17 events per individual) across 219 fruits (Mean = 4 fruits per

168 individual).

169   The behaviours were coded by one researcher using Windows Media Player. Inter-

170 coder reliability was evaluated with a second coder, based on 281 fruit-opening events (30%

171 of all events) for 29 subjects (Kappa = 0.91).

172   **Data analysis.** This study systematically examined fruit-opening behaviours by first

173   conducting an overall analysis, and then specifically compared chimpanzees across age

174   groups, sex groups, and the three colonies. As part of the overall analysis, we assessed

175   whether fruit-opening techniques were used in an organised manner. The applications of

176   opening techniques were measured during four consecutive and mutually-exclusive stages:

177   Initial opening (Stage 1), following initial opening, but before the first eating phase (Stage 2),

178   further opening a partially opened fruit (Stage 3), and following the first further opening

179   technique, but before additional eating phases (Stage 4). For descriptions and further details

180   on the stages and eating phases, see Table S2.

181   Age, sex, and colony comparisons were primarily conducted using generalized linear

182   mixed models (GLMM). GLMM analysis examines the effects of predictor variables, while

183   controlling for the potential non-independence of response variables. Response variables

184   were the mean number of combined technique types to completely open a fruit and the

185   percent number of fruits opened with a specific technique. The predictor variables were age

186   groups, sex groups, and colonies. Subject ID was included as a random effect. GLMM

187   analyses were only performed on models where the improvement of the fit between the full

188   and null models showed statistical significance. GLMM analyses were conducted using the

189   programme R version 2.15 (R Development Core Team 2010) with the "lme4" package

190   (Bates et al. 2010).

191   **Results**

192   **Overall analysis of fruit opening.** We distinguished eight distinct fruit-opening techniques

193   applied by subjects, including: half biting, full biting, fruit cracking, hitting on object, hitting

194   on ground, peeling, stomping, and throwing (for further details on the techniques, see Table

195   1). The first six techniques were found consistently across all age and sex groups. Of the

196   latter two techniques, only four instances of stomping and six instances of throwing were

197   observed, performed by two and one individuals, respectively. It is important to note that fruit

198   cracking was the only technique where fruits were used to open other fruits; specifically,

199   fruits were used as 'hammers' to strike against other fruits (see Figure 1 and Supplementary

200   video).

201   In total, nineteen subjects put fruits (N = 26) aside after applying a fruit-opening

202   technique, to eat in the future (Supplementary video). For 8 subjects, it was clearly visible

203   that these fruits were cracked open, with the pulp visible (14 fruits).

204   Table S3 provides an overview of the six most common techniques applied

205   throughout the four fruit-opening stages. The chimpanzees consistently used biting

206   throughout Stages 1-4 (Mean = 2.6 - 69.3% of techniques). Fruit cracking was present only in

207   Stages 1-3 (Mean = 13.2 - 19.9%). Hitting was primarily applied before the first eating phase,

208   in Stages 1-2 (Mean = 15.8 - 21.3%). In contrast, peeling was most frequently used after the

209   first or any additional eating phase, in Stages 3-4 (Mean = 9.7 - 18.3%).

210   **Fruit-opening techniques across age, sex and colonies.** GLMM analyses were first

211   conducted for combined techniques and then for specific technique types. For combined

212   techniques, collinearity between all GLMM predictor variables was low; the maximum

213   variance inflation factor (VIF) was 1.18. GLMM results showed that the chimpanzee colonies

214   differed significantly in the mean number of technique types combined to completely open a

215   fruit per subject ($P < .001$; see Table 2). Bonferroni corrected pairwise comparisons revealed

216   that chimpanzees in Colony 3 combined significantly more techniques than chimpanzees in

217   Colony 1 ($P < .001$) and Colony 2 ($P < .001$). No differences between sex and age groups

218   were found for combined techniques ($P > .05$; see Table 2).

9

219   For the GLMM analysis on specific techniques, Hommel-Hochberg corrections were

220   applied for repeated comparisons and α levels were adjusted. Results for the frequently-used

221   techniques, with the exception of peeling, are presented in Table 3. Peeling showed a non-

222   significant improved fit between the full and null models, and thus was excluded from

223   GLMM analysis. Collinearity between all GLMM predictor variables was low (maximum

224   VIF = 3.22). GLMM analysis revealed statistically significant differences across age groups

225   for hitting ($P < .001$) and tendencies of differences (Hommel-Hochberg corrections) in full

226   biting ($P = .048$) and fruit cracking ($P = .038$); see Table 3. No age differences were found

227   for half biting ($P > .05$). Bonferroni corrected pairwise comparisons showed that juveniles

228   used hitting on objects ($P < .001$) and hitting on the ground ($P < .001$) significantly more

229   often than adults and adolescents. GLMM analysis (with Hommel-Hochberg corrections)

230   revealed that the sex groups tended to show differences in half biting ($P = .025$); see Table 3.

231   No differences between sex groups were found for full-biting, fruit cracking, hitting on

232   ground or hitting on objects ($P > .05$). See Table S4 for the use of specific techniques across

233   age and sex groups for each colony.

234   In addition, GLMM analysis showed that the colonies differed significantly from each

235   other in the percent number of fruits the chimpanzees opened by using half biting ($P = .001$),

236   full biting ($P < .001$), and fruit cracking ($P < .001$); see Table 3 and Figure 2. Two of these

237   techniques were entirely absent in specific colonies. Full biting was not observed in Colony

238   3, but regularly occurred in Colonies 1 and 2 (produced by eleven and thirteen subjects,

239   respectively). Similarly, fruit cracking was absent in Colony 1, but was frequently observed

240   in Colonies 2 and 3 (produced by five and six subjects, respectively). Furthermore,

241   Bonferroni corrected pairwise comparisons showed that the chimpanzees from Colony 1

242   opened significantly more fruits with half biting than chimpanzees from Colony 2 ($P = .019$).

243

244 **Discussion**

245 The present study represents a non-experimental comparative assessment of the application

246 of natural foraging behaviours for opening hard-shell fruits across three chimpanzee colonies.

247 Analyses revealed fruit-opening differences across the three physically and socially separate

248 chimpanzee colonies in the number of combined techniques and the occurrence of three

249 specific techniques (half biting, full biting, and fruit cracking). Most strikingly, full biting and

250 fruit cracking were entirely absent in Colonies 3 and 1, respectively, yet present in the other

251 colonies. This study provides empirical evidence that behaviours underlying natural

252 extractive foraging, other than tool selection, can differ across primate colonies that have the

253 same foods available. The current findings thus supports previous findings on population-

254 specific foraging behaviours obtained from wild nonhuman primate communities, where

255 different resources were likely available (Whiten et al. 2001; van Schaik et al. 2003), and

256 where foraging behaviours have been measured under experimental conditions (Gruber et al.

257 2009; Biro et al. 2003; van de Waal et al. 2010).

258 Establishing whether asocial or social acquisition has occurred remains difficult in

259 field observations (Laland and Janik 2007). Here, the cross-colony differences in technique

260 application could not easily be explained as a result of asocial learning. If such learning had

261 occurred, then given the ecological similarity and comparable genetic composition, all

262 colonies should have exhibited similar fruit-opening behaviours. It is also important to note

263 that the three techniques which differed across colonies only involved the fruits and the

264 subjects' strength and skill. Thus, it appears that ecological factors do not account for the

265 cross-colony findings presented here.

266 Six opening techniques were used regularly by the chimpanzees. While *Strychnos*

267 fruit-opening behaviours have been reported (Gruber et al. 2010; Nishida and Turner 1996;

268 Boesch and Boesch 1990; McGrew 1999), the present work describes three techniques that,

269   to the authors' knowledge, not been reported previously in chimpanzees, including fruit

270   cracking, stomping and throwing. The latter two strategies appeared to be idiosyncratic

271   techniques, observed only in three individuals (stomping by two, throwing by one). While the

272   chimpanzees were fruit cracking, they were occasionally observed switching the 'hammer

273   fruit' so that it became the fruit to crack open (see Figure 1 and Supplementary video).

274   Observations also revealed some indication of food preparations, where nineteen subjects put

275   partially opened fruits aside, presumably to eat them later. These behaviours indicate further

276   flexibility in utilising hard-shelled fruits to extract food.

277   Despite exhibiting a range of flexibility, some of the techniques applied by the

278   subjects unfolded in an organised manner, with all techniques other than biting closely linked

279   to specific stages of the fruit opening process. Striking techniques (fruit cracking and hitting)

280   were primarily used to penetrate the fruit's outer shell prior to the first eating phase. These

281   powerful techniques gave way to peeling, a finer, dexterous behaviour used almost

282   exclusively after the first eating phase, which seems appropriate for removing the last shell

283   pieces. Previous field reports on primate feeding behaviours, including tool use, have

284   described similarly sophisticated levels of dexterity and organisation (Inoue-Nakamura and

285   Matsuzawa 1997; Russon 1998; Stokes and Byrne 2001; Byrne and Byrne 2001). Our results

286   also suggest that chimpanzees were displaying hierarchical mental construction – the capacity

287   to hold and integrate several cognitive, motoric or perceptual components to achieve the goal

288   (Stokes and Byrne 2001) – when opening hard-shelled fruits.

289   Interestingly, across all colonies, juvenile chimpanzees opened more fruits with

290   hitting techniques (i.e. on objects or the ground) than adolescent and adult subjects. Perhaps

291   young chimpanzees develop their own feeding methods for these hard-to-process foods to

292   compensate for the lack of adult/adolescent attributes, such as robust mandibular strength,

293   before acquiring adult/adolescent techniques. These findings contribute to the current

294   literature, where research on extractive foraging with tools has shown that immature

295   chimpanzees acquire feeding behaviours based on observing adult models (Inoue-Nakamura

296   and Matsuzawa 1997; Lonsdorf et al. 2004; Corp and Byrne 1991). Comparisons by sex

297   revealed that females tended to display more half biting than males, especially among the

298   adults and adolescents. These findings are consistent with field research showing sex-

299   differences in chimpanzee foraging behaviours (Goodall 1986; Lonsdorf 2005).

300   Consequently, it may be possible that such differences also extend to non-tool use foraging

301   conditions.

302   In summary, the current study examined natural, non-tool extractive foraging across

303   three separate chimpanzee colonies that had the same foods available and shared the same

304   environment conditions, as well as comparable phylogenetic backgrounds. From these

305   findings, we have concluded that chimpanzees may acquire their foraging behaviours from

306   within their social communities. Chimpanzees, like humans, live in complex social systems

307   and thus it is possible that learning specific foraging techniques and how to utilise them from

308   within the social group may have had an important role in shaping human culture among

309   early hominids. Previous field and captive studies have shown that primates are capable of

310   socially-mediated traditions (Dindo et al. 2008; Whiten et al. 2007; Reader and Biro 2010).

311   While such findings are important for expanding our knowledge of primate tool use and

312   social cognition, the current study, by observing large, semi-wild groups of chimpanzees,

313   provided a unique interface between field research and captive studies. Further, we believe

314   that studies of semi-wild primate groups are a valuable avenue of research to complement

315   existing methods in attempting to understand animal social learning and the evolution of

316   culture.

317

318

13

319

320 **Acknowledgements**

333

334

335 **References**

336 Agostini L, Visalberghi E (2005) Social influences on the acquisition of sex-typical foraging

337   patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigritus*).

338   Am J Primatol. 65: 335-351. doi: 10.1002/ajp.20120

339 Bates D, Maechler M, Bolker B (2010) lme4: Linear mixed effects models using S4 classes

340   (R package version 0.999375-35). http://CRAN.R-project.org/package=lme4.

341 Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sous C, Matsuzawa T (2003)

342   Cultural innovation and transmission of tool use in wild chimpanzees: evidence from

343   field experiments. Anim Cogn. 6: 213-223. doi: 10.1007/s10071-003-0183-x

344 Boesch C, Boesch H (1983) Optimisation of nut-cracking with natural hammers by wild

345   chimpanzees. Behaviour. 83: 256-286. doi: 1163/156853983X00192

346 Boesch C, Boesch H (1984) Possible causes of sex differences in the use of natural hammers

347   by wild chimpanzees. J Hum Evol. 13: 415-440. doi**:** 10.1016/S0047-2484(84)80055-

348   X

349 Boesch C, Boesch H (1990) Tool use and tool making in wild chimpanzees. Folia Primatol.

350   54: 1–15. doi: 0015-5713/90/0542-0086$2.75/0

351 Bonnie KE, Horner V, Whiten A, de Waal FBM (2006) Spread of arbritrary customs among

352   chimpanzees: a controlled experiment. Proc Roy Soc B. 274: 367-372. doi:

353   10.1098/rspb.2006.3733

354 Byrne RW, Byrne JM (1991) Hand preferences in the skilled gathering tasks of mountain

355   gorillas (*Gorilla g. berengei*). Cortex. 27: 521-546. doi: 10.1037/0012-1649.31.4.619

356 Crast J, Hardy JM, Fragaszy D (2010) Inducing traditions in captive capuchin monkeys

357   (*Cebus apella*). Anim Behav. 80: 955-964. doi: 10.1016/j.anbehav.2010.08.023

358 Corp N, Byrne R (2002) The ontogeny of manual skill in wild chimpanzees: Evidence from

359   feeding on the fruit of saba florida. Behaviour. 139: 137-168.

360 Davila-Ross M, Allcock B, Thomas C, Bard KA (2011) Aping expressions? Chimpanzees

361   produce distinct laugh types when responding to laughter of others. Emotion, 11:

362   1113-1120. doi: 10.1037/a0022594

363 Dindo M, Thierry B, Whiten A (2008) Social diffusion of novel foraging methods in brown

364   capuchin monkeys (*Cebus apella*), P Roy Soc B. 275: 187-193. doi:

365   10.1098/rspb.2007.1318

366 Fessler DM (2002) Dimorphic foraging behaviours and the evolution of hominid hunting. Riv

367   Biol. 95: 429-453.

368 Galef BG Jr. (2004) Approaches to the study of traditional behaviours of free-living animals.

369   Learn Behaviour. 32: 53–61. doi: 10.3758/BF03196006

370 Goodall J (1986) The chimpanzees of Gombe: Patterns of behaviour. Cambridge. MA

371   Harvard University Press.

372 Gruber T, Clay Z, Zuberbuhler K (2010) A comparison of bonobo and chimpanzee tool use;

373   evidence for a female bias in the Pan linage. Anim Behav, 80: 1023-1033. doi:

374   10.1016/j.anbehav.2010.09.005

375 Gruber T, Muller M, Strimling P, Wrangham R, Zuberbuhler K (2009) Wild chimpanzees

376   rely on cultural knowledge to solve an experimental honey acquisition task. Curr Biol.

377   19**:** 1806-1810. doi: 10.1016/j.cub.2009.08.060

378 Hopper LM, Schapiro SJ, Lambeth SP, Brosnan SF (2011) Chimpanzees' socially maintained

379   food preferences indicate both conservatism and conformity. Anim Behav. 81**:** 1195-

380   1202. doi: 10.1016/j.anbehav.2011.03.002

381 Horner V, Whiten A, Flynn E, de Waal FBM (2006) Faithful replication of foraging

382   techniques along cultural transmission chains by chimpanzees and children. PNAS.

383   103: 13878-13883. doi: pnas.0606015103

384 Inoue-Nakamura N, Matsuzawa T (1997) Development of stone tool use by wild

385   chimpanzees (*Pan troglodytes*). J Comp Psychol. 111: 159-173. doi: 10.1037/0735-

386   7036.111.2.159

387 Kendal RL, Custance DM, Kendal JR, Vale G, Stoinksi TS, Rakotomalala NL,

388   Rasamimanana H (2010) Evidence for social learning in wild lemurs (*Lemur catta*).

389   Learn Behav. 38: 220-234. doi: 10.3758/LB.38.3.220.

390 Koops K, McGrew WC, Matsuzawa T (2010) Do chimpanzees (*Pan troglodytes*) use

391   cleavers and anvils to fracture Treculia africana fruits? Preliminary data on a new

392   form of percussive technology. Primates. 51: 175-178. doi: 10.1007/s10329-009-

393   0178-6

394 Laland K, Janik VM (2007) The animal cultures debate. Trends Ecol Evol. 21: 542-547.

395 Lonsdorf EV (2005) Sex differences in the development of termite-fishing in the wild

396   chimpanzees *Pan troglodytes schweinfurthii* of Gombe National Park, Tanzania.

397   Anim Behav. 70: 673-683. doi: 10.1016/j.tree.2006.06.005

398 Lonsdorf EV, Eberly LE, Pusey AE (2004) Sex differences in learning in chimpanzees.

399   Nature. 428: 715-716. doi:10.1038/428715a

400 Lucas PW, Gaskins JT, Lowry TK, Harrison ME, Morrogh-Bernard HC, Cheyne SM, Begley

401   MR (2011) Evolutionary optimization of material properties of a tropical seed. J Roy

402   Soc Interf. 9: 34-42. doi: 10.1098/rsif.2011.0188

403 Luncz LV, Mundry R, Boesch C (2012) Evidence for cultural differences between

404   neighboring chimpanzee communities. Curr Biol. 22: 922-926. doi:

405   10.1016/j.cub.2012.03.031

406 Mackinnon KC (2006) Food choice by juvenile capuchin monkeys *Cebus capucinus* in a

407   tropical dry forest. New York, Springer, US. doi: 10.1007/0-387-25872-8_17

17

408 Matsumoto-Oda A, Kasagula MB (2000) Preliminary study of feeding competition between

409   baboons and chimpanzees in the Mahale Mountains National Park, Tanzania. Af Stud

410   Monogr. 21: 147-157.

411 McGrew WC (1979) Evolutionary implications of sex differences in chimpanzee predation

412   and tool use. In: The Great Apes in DA Hamburg and E McCown (Eds.),

413   Benjamin/Cummings Publishing, California. pp. 441-463.

414 McGrew WC (1999) Manual laterality in anvil use: Wild chimpanzees cracking *Strychnos*

415   fruits. Laterality. 4: 79-87. doi: 10.1080/03069887600760101

416 Nishida T, Turner L (1996) Food transfer between mother and infant chimpanzees of the

417   Mahale Mountains National Park, Tanzania. Int J Primatol. 17: 947-968. doi:

418   10.1007/BF02735296

419 Pruetz J, Bertolani P (2007) Savanna chimpanzees (*Pan troglodytes verus)* hunt with tools.

420   Curr Biol, 17, 412-417. doi: 10.1016/j.cub.2006.12.042

421 R Development Core Team. (2010) R: A Language and Environment for Statistical

422   Computing (Vienna: R Foundation for Statistical Computing).

423 Reader SM, Biro D (2010) Experimental identification of social learning in wild animals.

424   Learn Behav. 33: 265-283. doi: 10.3758/LB.38.3.265

425 Rosenberger AL, Hartwig WC (2011) New world monkeys. *Encyclopedia of Life Sciences*.

426   http://www.els.net Nature Publishing Group. Macmillan Reference Ltd.

427 Russon AE (1998) The nature and evolution of intelligence in orangutans (*Pongo pygmaeus*).

428   Primates 39: 485-503. doi 10.1007/BF02557571

429 Schoning C, Humle T, Mobius Y, McGrew WC (2008) The nature of culture: Technological

430   variation in chimpanzee predation on army ants revisited. J Hum Evol. 55: 48-59.

431   doi: 10.1016/j.jhevol.2007.12.002

432 Sterling E, Dierenfeld E, Ashborne C, Feistner A (1994) Dietary intake, food consumption

433   and nutrient intake in wild and captive populations of *Daubentonia madagascariensis*.

434   Folia Primatol. 62: 115-124.

435 Stokes EJ, Byrne RW (2001) Cognitive capacities for behavioural flexibility in wild

436   chimpanzees (*Pan troglodytes*): the effect of snare injury on complex manual food

437   processing. Anim Cogn. 4: 11-28. doi: 10.1007/s100710100082

438 Tennie C, Call J, Tomasello M (2009) Ratcheting up the ratchet: On the evolution of

439   cumulative culture. Phil Trans Roy Soc B. 364: 2405-2415. doi:

440   10.1098/rstb.2009.0052**.**

441 Tutin CEG, Baillie JEM, Dupain J., Gatti S, Maisels F, Stokes EJ, Morgan DB, Walsh PD

442   (2008) *Pan troglodytes* ssp. *troglodytes*. In: IUCN 2013. IUCN Red List of

443   Threatened Species.

444 van Lawick-Goodall, J, Van-Lawick H, Packer C (1973) Tool-use in free-living Baboons in

445   the Gombe National Park, Tanzania. Nature. 241: 212-213. doi:

446   doi:10.1038/241212a0

447 van de Waal E, Renevey N, Favre CM, Bshary R (2010) Selective attention to philopatric

448   models causes directed social learning in wild vervet monkeys. Proc Roy Soc B. 277:

449   2105-2111. doi: 10.1098/rspb.2009.2260

450 van de Waal E, Claidièrea N, Whiten A (2013) Social learning and spread of alternative

451   means of opening an artificial fruit in four groups of vervet monkeys. Anim Behav.

452   85: 71-76. Doi: 10.1016/j.anbehav.2012.10.008

453 van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton L, Suzuki A,

454   Utami SS, Merill M (2003) Orangutan Cultures and the evolution of material culture.

455   Science 299: 102-105. doi:10.1126/science.1078004

19

456   van Schaik CP, Knott, CD (2001) Geographic variation in tool use on Neesa fruits in

457   orangutans. Am J Phys Anthropol. 114: 331-42.

458   Whiten A, Goodall J, McGrew W, Nishida T, Reynolds V, Sugiyama Y, Tutin C, Wrangham

459   R, Boesch C (2001) Charting cultural variation in chimpanzees. Behaviour. 138**:**

460   1481-1516. http://dx.doi.org/10.1163/156853901317367717

461   Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth SP, Schapiro SJ, de Waal FBM (2007)

462   Transmission of multiple traditions within and between groups. Curr Biol. 17: 1-6.

463   doi: 10.1016/j.cub.2007.05.031

464   Whiten A, Goodall J, McGrew WC, Nishida T, Reynoldsk V, Sugiyama Y (1999). Culture in

465   chimpanzees. Nature. 399: 15-19. doi:10.1038/21415.

466   Wilson M L, Balmforth Z, Cox D, Davenport T, Hart J, Hicks C, Hunt K D, Kamenya S,

467   Mitani J C, Moore J, Nakamura M, Nixon S, Plumptre A J, Reynolds V (2008). *Pan*

468   *troglodytes* ssp. *schweinfurthii*. In: IUCN 2013. IUCN Red List of Threatened

469   Species.

470

471

472

473 **Figure Captions**

474 **Figure 1. Switching fruits while fruit cracking:** An adult male chimpanzee used the fruit cracking

475 technique, i.e., used one fruit as a 'hammer' to crack open another fruit (a, b), before visually

476 inspecting it. Then, he put the latter fruit away (c), placed the 'hammer' fruit into his left hand (d),

477 selected another fruit to use as a 'hammer' (e), and continued with the fruit cracking (f).

478

479 **Figure 2. Fruit-opening across colonies:** Significant differences were found for the number

480 of fruits opened with half biting ($P < .001$), full biting ($P < .001$), and fruit cracking ($P <$

481 $.001$) events measured for every subject across the three colonies.

482

21