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Resilience of experimentally-seeded dietary traditions in wild vervets: evidence from group fissions

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1   **Resilience of experimentally-seeded dietary traditions in wild vervets: evidence from**

2   **group fissions**

3

4   **Short title:**

5   **Resilience of traditions in wild vervets**

6

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22 **Abstract**

23 Controlled laboratory experiments have delivered extensive and compelling evidence for the

24 diffusion and maintenance of socially learned behavior in primates and other animals. Such

25 evidence is rarer in the wild, but we show that a behavior seeded in a majority of individuals

26 within vervet monkey (*Chlorocebus pygerythus)* groups may be sustained across several

27 years. Here we report results of two natural fission events in such groups that offer novel

28 evidence of the resilience of socially-transmitted group norms of behavior. Before fission,

29 high ranked females exhibited an almost exclusive adherence to a group preference among

30 two food options, originally introduced through a distasteful additive in one option, but no

31 longer present in repeated later tests. Because of rank-dependent competition, low-ranked

32 females ate more of the formerly distasteful food and so discovered it was now as palatable as

33 the alternative. Despite this experience, low ranked females who formed the splinter groups

34 then expressed a 100% bias for the preferred option of their original parent group, revealing

35 these preferences to be resilient. We interpret this effect as conformity to either the

36 preferences of high rankers or of a majority in the parent group, or both. However, given

37 fissioned individuals' familiarity with their habitat and experimental options, we question the

38 adequacy of the informational function usually ascribed to conformity and discuss alternatives

39 under a concept of 'social conformity'.

40

41 **Keywords:**

42 Social learning, group fission, tradition, field experiment, conformity

43

44 **Introduction**

45 A wealth of experimental studies has now demonstrated the social learning of foraging habits

46 and other behavior patterns in primates and in a wide variety of other species [Aisner &

47 Terkel, 1992; Galef, 1996; Galef & Whiten, 2017; Leadbeater & Chittka, 2009; Whiten, 2012;

48 van de Waal, Claidière, & Whiten, 2013a; Zentall, 2012]. Such evidence is often strongest in

49 laboratory or other captive contexts where experimental controls are most tractable to arrange,

50 most importantly the provision of opportunities to learn from a model performing a novel

51 action, contrasted with a no-model control condition, and/or to learn from either of two

52 models displaying different behaviors. However, in the service of better understanding the

53 implications of such social learning in the natural lives of animals, a small but growing

54 number of experiments following these and other designs have now been engineered in the

55 more challenging circumstances of the wild, providing evidence of social learning in a range

56 of primates [Gunhold, Massen, Schiel, Souto, & Bugnyar, 2014a; Gunhold, Whiten, &

57 Bugnyar, 2014b; Kendal et al., 2010; Schnoell & Fichtel, 2012; Schnoell, Dittmann, &

58 Fichtel, 2014; van de Waal, Renevey, Favre, & Bshary, 2010; van de Waal & Bshary, 2011;

59 van de Waal, Borgeaud & Whiten, 2013b] and other mammalian and avian species [Aplin et

60 al., 2015; Slagsvold & Wiebe, 2011; Thornton & Clutton-Brock, 2011]. Additionally, new

61 statistical techniques like social network diffusion analyses have offered complementary and

62 compelling evidence for social learning in wild birds [Aplin et al., 2015], primates [Hobaiter

63 Poisot, Zuberbühler, Hoppitt, & Gruber, 2014] and cetaceans [Allen, Weinrich, Hoppitt, &

64 Rendell, 2013].

65

66   Social learning of diet and foraging behavior revealed in these studies creates the

67 potential for diffusion of innovations that may spread to become traditions (group typical

68 behavior shared by group members that relies on social learning), ranging from the short term

69 to longer-term cases that may survive across generations [Mercader et al., 2007]. The

70 evidence for animal traditions is also growing, yet remains more limited than for social

71 learning *per se,* in part because the research required is inherently more demanding than the

72   basic 'A learns from B' paradigm that can be sufficient to identify social learning.

73   Experimentally identifying the diffusion of socially learned behaviors necessarily involves

74   tracking the spread across multiple individuals. Diffusion experiments of this sort have begun

75   to proliferate, again particularly in the most readily controlled laboratory and other captive

76   conditions [reviews: Mesoudi & Whiten, 2008; Whiten, Caldwell, & Mesoudi, 2016]. In one

77   approach, called transmission or diffusion chains, a novel behavior is seeded in a founder

78   model, who is then observed by a second individual who in turn becomes a model for the

79   next, a process repeated to track transmission over multiple potential 'cultural generations'. A

80   small set of such studies has identified transmission over as many as 6-8 such 'generations' in

81   birds [Curio, Ernst, & Vieth, 1978], rodents [Laland & Plotkin, 1990] and primates [Dindo,

82   Thierry, & Whiten, 2008; Horner, Whiten, Flynn E, & de Waal, 2006].

83

84   The control necessary to engineer such a linear series has, to our knowledge,

85   unsurprisingly defied implementation in the wild. Instead an alternative approach called 'open

86   diffusion' has been more feasible in the wild as well as in captivity [Whiten et al., 2016]. In

87   this approach, founder models are trained to perform alternative behavioral solutions to

88   naturalistic foraging problems and allowed to perform these within their group, with it being

89   'open' who watches and potentially learns from what is modelled, and the subsequent

90   behavior of observers is subsequently monitored through further experimental presentations.

91   Although only a few such studies have been completed in the wild, they have delivered

92   positive evidence of diffusion, in birds [Aplin, Sheldon, & Morand-Ferron, 2013; Aplin et al.,

93   2015], meerkats [Thornton & Malapert, 2009a] and monkeys [van de Waal, Claidière, &

94   Whiten, 2015]. However the evidence for longevity in the alternatives that start to diffuse, and

95   hence form incipient traditions, is more mixed. In many such studies the seeded options tend

96   initially to be copied, but individuals' discovery of the alternative option may then erode the

97   behavioral differences over time, such that stable alternative traditions are not necessarily

98   sustained [Kendal et al., 2010; Schnoell & Fichtel, 2012; Thornton & Malapert, 2009b; van de

99   Waal et al., 2015].

100   Given evidence for a basic form of 'conformity' in animal social learning, whereby

101   individuals show an adaptive bias to 'copy the majority' [Claidière & Whiten, 2012; Haun,

102   van Leeuwen, & Edelson, 2013], the spread and stabilization of seeded innovations in such

103   experiments may be an example of social learning that is inherently limited by a reluctance to

104   copy relatively rare behaviors, or behaviors shown only by only one or a few individuals.

105   Given this consideration, van de Waal and colleagues [2013b] explored an alternative

106   approach in which whole groups of vervet monkeys were seeded with alternative behavioral

107   options and the responses of naïve individuals experiencing these apparent existing traditions

108   were recorded. In this case the alternative behaviors involved preferring to eat maize of one

109   color, and avoiding another color that signaled an aversive and bitter taste. Once the two

110   provisions were later made equally palatable, the social learning responses of two categories

111   of naïve others (new infants and migrating mature males) were recorded. In both infants and

112   immigrant males, potent social learning was found, consistent with a 'copy the majority' bias

113   noted above, especially in the case of the migrant males [Whiten & van de Waal, 2016]. This

114   effect therefore offers an important context in which to further investigate the resilience of

115   experimentally seeded traditions once they are common in the group. In this paper we report

116   the results of repeated testing over a period of 22 months.

117

118   Events in which small groups of low-ranking females split off from one large group,

119   which occurred on two different occasions, are of particular interest here because of the

120   behavior they later revealed. Female vervet monkeys have a strict linear dominance arranged

121   according to matrilines within each group [Cheney & Seyfarth, 1990]. We observed

122 permanent group fissioning from our largest group (over 50 individuals before the first

123 fission) Baie Dankie (BD). The 'In Betweeners' (IB) was the first splinter group from BD

124 during our three years of studying four groups of vervet monkeys, and Intaka (IN) group was

125 the second to split from BD, after four years of studying these four groups. Since 2014 the

126 field site has experienced a drought, so fissions may occur when food resources are scarce and

127 the group has become too large to share these well. In the pioneer and only long term study

128 of a vervet monkey population in the Amboseli Park in Kenya, group fusions were

129 documented [Jaffe & Isbell, 2010], but not group fission [Robert M. Seyfarth. pers. comm.].

130 To our knowledge we report here the first fissions in vervet monkeys. However dispersal by

131 the fissioning of an established group is well-documented in many other old world monkeys

132 [e.g., blue monkeys: Cords & Rowell, 1986; Cords, 2012; redtail monkeys: Struhsaker &

133 Leland, 1988; Japanese macaques: Koyama, 1970; Sugiyama, 1960; rhesus macaques:

134 Chepko-Sade & Sade, 1979; long-tailed macaques: van Schaik & van Noordwijk, 1988; and

135 savannah baboons: Nash, 1976].

136

137 As we show below, because of their low rank in the parent group, the individuals in

138 our splinter groups had earlier gained significant personal evidence that both food colors

139 denoted palatability and edibility. The fact that low rankers are more opportunistic and

140 flexible in their feeding behavior than high rankers was nicely demonstrated in cooperatively

141 breeding birds [Keynan, Ridley, & Lotem, 2015]. The individuals that we studied in the

142 fissioned groups therefore provided a particularly pointed test of the effects of social learning

143 on long-term behavioral biases: would females in these splinter groups, who already deviated

144 most from the predominant pattern in their group, be the most likely to show further

145   degradation of the seeded bias in color preference? Or would they now more freely express

146   this bias, such that it would be traditionally maintained in the new groups?

147

148   **Methods**

149   *Study populations and field site*

150   The study was conducted between August 2011 and September 2014 as part of the Inkawu

151   Vervet Project (IVP) in a 12,000-hectares private game reserve, "Mawana", in KwaZulu

152   Natal, South Africa (S 28° 00.327; E 031° 12.348).

153   Subjects were vervet monkeys, *Chlorocebus pygerythus*, in six habituated groups; four

154   main groups and two splinter groups that divided from these. Such division is often referred to

155   in the literature as group fission, but here we prefer the term 'splinter' to denote that two very

156   small groups were created, leaving behind one still-large group. Aside from these small

157   splinter groups, monkeys lived in stable groups which varied from 24 to 56 individuals. In our

158   population, all groups are distributed along a river, and each group's home range overlaps

159   with those of multiple neighboring groups. Average home range size was ca. 160 hectares.

160   Groups typically contained an alpha male, subordinate males and several matrilines (females

161   and their offspring). Male vervets migrate to other groups when they are sexually mature

162   (usually around 4 years of age), while females usually remain in their natal group throughout

163   their lives. Vervet monkeys have a linear dominance hierarchy manifested in relation to

164   matrilines within the group; high-ranking females and their close relatives (mothers, sisters,

165   and daughters) are the most sought-after grooming partners [Isbell, Pruetz, Lewis, & Young,

166   1999]. High-ranking females enjoy priority access to food during foraging bouts and have

167   access to higher quality food, which greatly increases their yearly food intake compared to

168   lower- and mid-ranking females [Whitten, 1983]. The dominance hierarchy at IVP is assessed

169   by the creation of matrices based on dyadic aggressive interactions (i.e., winner- loser)

170 occurring either in a natural context or around various food experiments. Using the "I&SI"

171 method of de Vries [1998], we found that the female hierarchy was stable during the study

172 period whereas the male one was highly variable [Borgeaud, Sosa, Sueur, Bshary, & van de

173 Waal, 2016].

174   The present study focused on two recent group splits in the largest group (including a

175 maximum of 56 individuals during this study) of our study population. First, in 2012, six

176 individuals left 'Baie Dankie' (BD) group and formed the 'In-Betweeners' (IB) group; a year

177 later, in 2013, three other individuals left BD group and formed the 'Intaka' (IN) group (Fig. 1

178 and Table 1; more details in results section). We considered each splinter group as

179 independent from their origin group, once they had been sleeping in different sleeping sites

180 than their origin group for over a month, and encounters with their origin groups were

181 agonistic, similar to those with other neighboring groups. Therefore the splinter groups had no

182 opportunities for observational learning from their original group after they fissioned. All

183 individuals were identified, mainly by facial cues. A recognition file with portrait photographs

184 as well as specific individual features (scars, color, etc) was maintained for each group.

185

186 *Experimental procedure*

187 The initial training phase consisted of three sessions, conducted at monthly intervals, where

188 two adjacent boxes of maize, one dyed blue and one pink, were offered to the monkeys. Both

189 boxes of maize where soaked overnight in plain water with food coloring in it, and in one box

190 of maize mountain aloe (*Aloe marlothii*) leaves were added giving it a very bitter taste and

191 smell, unpalatable for the monkeys. For two groups the aloe-treated maize was dyed blue

192 ('Lemon Tree' (LT) and 'Noha' (NH) groups), for two others, pink ('Ankhase' (AK) and BD

193 groups). These training sessions provided about 2 kg of maize for the groups, that ranged

194 from 30 to 43 individuals during the three training sessions, so less than 70g per individual on

195 average. Boxes were refilled to ensure that monkeys always had a choice and that as many

196 group members as possible participated. Training and test sessions were unrestricted in time,

197 lasting as long as individuals were feeding so as to have as many group members as possible

198 participating (for the initial six tests in the four large groups pre-fission: minimum length

199 97min, maximum length=4h32min; the splinter group trials: IB=31min, IN=43min).The side

200 of the pink and blue maize was alternated across the three training sessions and the six test

201 trials, as viewed from the camera and researchers' perspective.

202   The subsequent experimental phase for the four trained groups consisted of six test

203 trials spaced at intervals of 1, 1, 2, and 4 weeks, then approximatively 6 months, with two

204 boxes containing the same two colors of soaked maize, but with one major exception: no

205 maize was aloe-treated. Thus, all maize was now palatable and edible. Observational data

206 were collected only 48h after each provisioning [van de Waal et al., 2013b].

207   After each of the two group fissions noted above, we tested the new splinter group on

208 its own as soon as possible, which took several months to achieve. The new groups did not

209 include any individual with a VHF collar so were not easy to locate, in addition to which they

210 were highly mobile in establishing their new home range and avoiding large neighboring

211 groups. They were also relatively shy so testing was delayed until winter when they were

212 most motivated to participate in test sessions. As a result tests occurred seven months after

213 fission for IB group, and over a year later for IN group.

214   As both group splits occurred in the same group, BD, which had earlier been trained to

215 eat blue maize, we designed an additional test to investigate low-ranking females in a pink-

216 trained group. We conducted these experiments on the seven lowest-ranked females of NH

217 group, a group well habituated to human researchers. We targeted each of these females while

218 she was alone (or just with her own offspring) and offered her a small box with two

219 compartments filled with the two colors of maize. We conducted these experiments at the end

220 of the South African winter in September 2014, when the natural food of the vervet monkeys

221 is scarce, and the monkeys spread out after they leave the sleeping site. We presented the food

222 for a maximum of 10 minutes or until other group members approached.

223

224 *Data collection and analyses*

225 All experiments were recorded using a video camera on a tripod. The image included the two

226 boxes and approximately 1 meter on each side. In addition, on each minute we recorded who

227 was eating at the boxes. A minimum of two observers conducted and recorded the

228 experiments in the four trained groups. As the splinter groups were relatively shy to human

229 observers we initially conducted the experiments with the camera on a tripod without any

230 researchers nearby, and later with only one researcher in IB group, then initially with only one

231 researcher, then two, in the IN group.

232 We applied a focal sampling method during the field experiments, and where

233 necessary in supplementary video analysis, to record each individual processing (eating or

234 spitting out) up to seven pieces of maize of each color per session. Coding was unambiguous

235 as it was always conducted when feeding individuals were facing the observers and the color

236 of the maize was easily visible.

237 All statistical analyses were performed using IBM SPSS 22. Because the splinter

238 groups provided only small sample sizes, two-tailed non-parametric analyses are applied

239 throughout. Non-parametric tests are robust for our multiple measures on the same individuals

240 [Chen & Popovich, 2002].

241

242 *Ethics*

243 The experimentation reported in this paper followed the American Society of

244 Primatologists' Principles for the Ethical Treatment of Primates. The study was registered

van de Waal et al.
11

245　with Ezemvelo KZN Wildlife in South Africa and the experiment including use of aloe to

246　create a distasteful sample of food was approved by the Ethics Committee of the School of

247　Psychology and Neuroscience, University of St Andrews.

248

249　**Results**

250　*Rank predicts adherence to modal group preferences*

251　Following the original 2011 aloe training described above, we offered the choice of the two

252　colors of maize, now untreated and thus palatable, in repeat tests run up to 2014. We found

253　that a strong correlation had emerged between the percentage of time that a female spent

254　eating the locally preferred color and her rank in the group's dominance hierarchy, with the

255　highest-rankers exclusively eating the original, always palatable color and ignoring the

256　originally aloe-tainted, but now equally palatable, alternative (Spearman correlation, N=26

257　(the females who participated in all 6 trials), Rho= -0.730, P<0.001; Fig. 1a, see

258　supplementary Fig. 1 and video 2; Spearman correlation, N=36 (all females that participated

259　at least in 1 trial), Rho=-0.447, P=0.006). Inspection of individual profiles (Fig. 1b) indicated

260　that this effect was mainly caused by the lowest ranked females in each group (boxed in

261　figure), who in the competitive context of the maize provisioning, took much more of the

262　originally distasteful but now perfectly palatable color of maize (Fig. 1b).

263

264　*Change in expressed preferences of fissioned groups females*

265　The recent group fissions documented above revealed a prioritization of social over personal

266　information. These fissions occurred after the behavioral patterns illustrated in Fig. 1 were

267　established. Both small splinter groups (see Table 1 for individual details) came to occupy

268　home ranges that overlapped that of the parent group, BD (Fig. 2).

269   Comparing the time spent eating blue versus pink maize before vs. after the group

270   fissions we found a significant change in color choices. Although all IB females ate both

271   colors in the original BD group (individual Oo is a male, see Table 1), they ate exclusively

272   blue maize during the first test after having separated from the higher rankers of their original

273   group, whose members displayed a strong preference for blue maize. The IN females

274   similarly ate both colors while still in BD but ate only blue maize during the first test after the

275   fission (Wilcoxon signed-rank test of change in percentage of blue taken, including (i) all

276   individuals of both splinter groups: Wilcoxon signed-rank test, N=9, Z=-2.52, P<0.02, and (ii)

277   with only the adult females of both splinter groups: Wilcoxon signed-rank test, N=6, Z=-2.20,

278   P<0.05; Fig. 3a, b, see supplementary Fig. 3).

279   The strong bias of these females towards the majority preferences of the parent BD

280   group occurred despite the fact that all had substantial direct, prior personal experience that

281   both foods were equally palatable (and some had equal or even more experience with the

282   locally non-preferred color), for they had fed on pink maize in repeated but separate episodes

283   during an average of 9.2 one-minute samples (s.d ± 3.3) spread across the experimental trials,

284   before the fission events (details in Table 2).

285

286   *Control test excluding basic color preference*

287   Further analyses explored and tested potential explanations for the bias. First is the possibility

288   that vervet monkeys simply have a basic preference for blue over pink food items. Because no

289   splits occurred in pink-trained groups, which would have provided cross-confirmation of the

290   results from the blue trained group, BD, we tested the seven lowest-ranking females in the

291   two pink-trained groups while they were not in association with higher-ranking competitors,

292   offering the small boxes with compartments of pink and blue maize, as described above. We

293   found an all-but-exclusive preference for pink in these solo tests (percentage time spent eating

294   this preferred color: N=7, median = 100 and mean = 99.7), much stronger than these same

295   females had expressed in earlier group tests (Wilcoxon signed-rank test, N=7, Z=-2.20,

296   P<0.05; Fig 4, see also supplementary Fig. 4 and video 5). This finding confirms there is no

297   general bias towards a preference for blue maize. These results are also consistent with those

298   observed after the group splits (i.e. that low-rankers prefer the majority choice, even if they do

299   not, or cannot, select it in a group setting).

300

301   *Confirmation of a socially learned effect*

302   A second analysis served to examine the possibility that once females had split from higher-

303   ranked group mates, the strong preference they expressed could simply be one all monkeys

304   had learned individually from their original training experience of aloe-treated food, and

305   could return to now that they had the opportunity to do so. This scenario is not supported

306   because we found that only one of the six females forming the IB and IN groups had taken

307   treated maize into her mouth during the original training events. Moreover, only one of the

308   seven low-ranking females in the pink-trained group (NH) that were tested alone ate one piece

309   of aloe-treated maize, a single time. More generally, of the 39 females from our four groups

310   present during the original aloe training, only 20 directly sampled aloe-treated maize

311   (meaning taken in hand or mouth a piece of maize), and a similar number, 19, never touched a

312   piece of the aloe-treated maize. These 19 females that had never smelled or tasted the treated

313   maize subsequently ate for a mean percentage of time intervals 86.6% of blue maize in the

314   blue trained groups and 16.2% in the pink trained groups during 6 pre-fission tests,

315   percentages not significantly different from the 77.6% and 13.6% respectively, for the 20

316   females that had learned by direct experience of treated maize (Mann-Whitney U test, N=39,

317   U=181.5, P=0.811; Fig. 5a, b). These results indicate that for half of all the females in our

318   experiments, the persistent preference they expressed was not based on their own past direct

van de Waal et al.
14

319   experience, but instead on social learning, likely resulting from often strong observational

320   cues that one alternative was very distasteful, such as monkeys throwing pink maize away or

321   spitting it out. Encounters of the splinter groups with neighboring groups, even with their

322   original group, were always aggressive. Accordingly they could never observe other groups

323   feeding on the colored maize, so there were no further opportunities for social learning. The

324   color preference must have been derived from pre-fission learning.

325   Results from a group tested with no aloe training underline the resilience that vervets

326   may display once a dietary preference is expressed by a majority. When this group, Kubu,

327   was offered the two colors of maize, the alpha male started eating pink, but the alpha female

328   started eating blue. The alpha male ate first, then the alpha female came and ate when the

329   alpha male was still eating. She was joined by two others that also ate blue. Then both alphas

330   left and the four other monkeys started eating blue. The alpha male ate only pink during the

331   first trial, but then he switched and ate only blue at the second trial, and maintained a

332   preference for blue in the following trials up to the seventh trial. Over the course of seven

333   tests this group, that never tasted any bitter-tasting aloe maize, displayed as strong and

334   resilient a preference for one color as the aloe trained groups (mean percentage of time eating

335   preferred color over trial 1 to 7, in the four trained groups = 70.4% ; in Kubu group = 69.2%).

336

337   *Copying high-rankers or a majority?*

338   A third and final issue is whether the social learning effect is based on the monkeys'

339   observation of just one or a few individuals, such as high ranked animals, or the alternative of

340   copying a majority (a criterion for 'conformity' preferred by many [Battesi, Moreno, Joly, &

341   Mery, 2012; Henrich & Boyd, 1998; van Leeuwen & Haun, 2013; van Leeuwen & Haun,

342   2014; Pike & Laland, 2010] though not all authors [van de Waal et al., 2013b]. As Fig. 1

343   shows, a bias to copy the highest-ranked animals could produce a similar effect to copying the

344   majority and we cannot definitively distinguish these. However, we found that the array of

345   monkeys that others could view was consistently and repeatedly displaying a clear majority at

346   one of the two colors (Fig. 6a), and that the cumulative majority of individuals eating blue

347   that monkeys could easily have observed before the group splits rose steadily during the

348   experiments (Fig. 6b). Thus information that could inform conformity was clearly readily

349   available. In the discussion we explain why perception of these majority displays and

350   conformity to them may offer the most parsimonious explanation for the behavior of the

351   splinter group females.

352

353   **Discussion**

354   The six females in the two splinter groups, tested several months after the split, showed a

355   100% bias for the dietary preference shown by a majority of their parent group, and we have

356   presented data rejecting the possibility that this reflects an inherent color preference or an

357   earlier, individually learned preference. Accordingly these results lead us to conclude that the

358   strong preferences are socially learned traits. The existence of such dispositions could

359   potentially thus support traditions resilient to major perturbations in the social fabric of groups

360   such as the fissions we documented. Given that only one of the fissioning females had ever

361   directly mouthed aloe-treated maize and that all these individuals had direct experience that

362   both colors were palatable and had no side effects, their 100% commitment to their origin

363   group color preference is striking.

364

365   An explanation for the strength of this effect might lie in the fact that ours is so far the

366   only study to seed local habits in a *majority* of each group. The handful of other field

367   experiments that have seeded alternative behaviors in the wild have typically done so in only

368   single individuals initially, and these studies have tended to demonstrate initial social

369 learning, soon followed by corruption and erosion of group behaviors, rather than the

370 resilience so marked in our own study where we instead simulated existing customary

371 traditions [Kendal et al., 2010; Schnoell & Fichtel, 2012; Thornton & Malapert, 2009b; van

372 de Waal et al., 2015]. Another potential explanation is that our experiment is the only one

373 testing a preference for a food type rather than including an object or 'artificial fruit'

374 manipulation like those cited above. Using social information to make adaptive food choices

375 may be a more habitual process than learning manipulative techniques.

376

377 What decision rules of these females explain such effects? Two principal options

378 appear to fit our findings. One is that the fissioning females were motivated to try to act like

379 the highest ranked females they had witnessed in their parent group, who expressed the

380 strongest preference for the maize color favored by the group (Fig. 1). Such preferential

381 copying of high ranked individuals has been shown in captive primates (chimpanzees) and

382 suggested to be adaptive insofar as high ranking individuals are often the most successful

383 foragers and therefore best to copy [Kendal et al., 2015; Horner, Proctor, Bonnie, Whiten, &

384 de Waal., 2010]. In the wild, Hobaiter and colleagues [2014] found evidence of a dominant

385 individual (the alpha male) seeding a behavior (using moss for water sponging) in a

386 chimpanzee community, and this has now spread further [Lamon, Neumann, Gruber, &

387 Zuberbühler, 2017]. However to our knowledge, such an effect has not been shown

388 experimentally in the wild, to date. If this motivation was responsible for the effect, it

389 survived the severing of the association with these high ranking females by at least 4 months.

390

391 A second alternative is adopting the preference shown by a majority of the parent

392 group, a form of conformity [Haun et al., 2013], although in this case based on long term

393 memory of majority behavior in the parent group, BD. Such effects have been documented in

394   other animals including birds [Aplin et al., 2015], and male migrants in our own study

395   population [van de Waal et al., 2013b; Whiten & van de Waal, 2016]. In the results section we

396   documented that there was a visible majority available for the individuals to copy the color

397   choice before they fissionned (Fig. 6). However as it was logistically not feasible in the field

398   to gather data on the attention of bystanders around the colored food, we cannot discriminate

399   if this was key in the current study. We do think it feasible to experimentally test for a bias to

400   copy high rank models in future, although this is far from straightforward to engineer. We

401   suggest that of the two potential rules, this would thus appear to be the more cognitively

402   economic to implement, compared to one that requires integration of (i) knowledge of the

403   ranks of group mates; (ii) a running tally of the preferences of each and (iii) a comparison of

404   these tallies. We know that resident vervet monkeys do in fact acquire a good working

405   knowledge of rank relationships in their group [Borgeaud. van de Waal, & Bshary, 2013;

406   Seyfarth & Cheney, 2015], so this hypothesis deserves to be investigated and experiments to

407   do so are ongoing in our research program. In the meantime, copying the majority appears the

408   most parsimonious of the two processes likely to underlie the resilience our data demonstrate.

409   Of course the two potential rules are not mutually exclusive: both may be in operation here

410   and may mutually reinforce each other to maintain group traditions long after the original

411   conditions that created them have passed. Either way, the mechanisms involved produced a

412   remarkable resilience in the preferences established through social learning, even after major

413   changes in social context and in the face of personal information that could have led to an

414   erosion of these preferences.

415

416   A major issue therefore concerns what functions such resilient group-level preferences

417   may serve. Here we suggest that a distinction between what social psychologists call

418   informational versus normative conformity provides a helpful framework [Claidière &

van de Waal et al.
18

419   Whiten, 2012; Deutsch & Gerard, 1955]. Informational conformity serves the function of

420   providing good, truthful information about the world; in the present context this concerns

421   which is the best of two food options to consume. Normative conformity, by contrast, serves

422   purely social functions, such as strengthening bonds with others by simply being more like

423   them, or adhering to societal or even prescribed norms. In our experiment, copying either

424   high rankers or a majority of others might in principle serve an informational function, insofar

425   as high rankers tend to eat the 'best' foods, and a majority of the group has likely converged

426   on the optimal choice too. However, neither of these rationales fit well with the circumstances

427   of the fissioning females, who already had good personal information on the palatability and

428   safety of eating either of the food colors on offer. Moreover, unlike the male migrants for

429   whom we earlier reported conformity to the new and different preferences of their adopted

430   group [van de Waal et al., 2013b] and so perhaps had need of local adaptive information, the

431   females had not moved far, partly occupying the same familiar area, and even sometimes

432   feeding on the same provisioning sites as before.

433

434   Accordingly we suggest we should explore the hypothesis that the females' behavior

435   could constitute what we here provisionally call 'social conformity'. By social conformity we

436   mean that individuals act like others not to achieve an informational function, but instead to

437   achieve a social function that derives from simply 'being like others' as suggested by the

438   bonding and identification-based observational learning (BIOL) theory [de Waal, 2001],

439   despite other options being open to them (in the present case, selecting only one of two food

440   options they know are equally palatable). Such a disposition may need no underlying complex

441   cognition, but merely the following of a motivational rule, that might have innate or learned

442   origins or both. If the rule were to preferentially act as the majority do, such conformity could

443   normally assist intra-group integration, important for a range of outcomes including

444   coordinated travelling and foraging, and mating opportunities. If the rule were to

445   preferentially act as high-rankers do, such conformity could make performers appear of

446   superior status (we are aware that referring to conformity here deviates from the common

447   usage denoting copying a majority), but we apply it to highlight that the individual would be

448   ignoring alternative actions open to it and copying 'just to be like others', another common

449   way in which the term conformity is used.

450

451   'Social conformity' thus contrasts with informational conformity in a similar way as

452   does social psychologists' 'normative conformity', but we use a different term because

453   normative conformity is often taken to require a recognition that norms *should* be followed

454   (i.e. that norms are prescriptive and deviations may be punished), although in fact some

455   psychologists in any case divide norms into either prescriptive norms (what it is proper to do)

456   or merely descriptive norms, which describe the statistical property of what a majority do

457   (easily applied to non-human animals, as indeed we do here). In children recognition of the

458   prescriptive, normative aspect of conformity emerges early in childhood, as in experiments

459   where, for example, children object when a peer or even a puppet transgresses an arbitrary

460   conventional norm [Keupp, Behne, & Rakoczy, 2013; Rakoczy, Warneken, & Tomasello,

461   2008].

462

463   We speculate that the more elementary possibility we have called social conformity

464   may nevertheless turn out to be a significant phenomenon in nature, given the importance for

465   group-living animals of meshing one's social dealings with others [Silk, Alberts, & Altmann,

466   2003; Silk, 2007; de Waal & Lutrell, 1986]. There is evidence that primates are more

467   affiliatively disposed to those who match their own behavior [Nielsen, Collier-Baker, Davis,

468   & Suddendorf, 2005; Paukner, Anderson, Borelli, Visalberghi, & Ferrari, 2005; Paukner,

469 Suomi, Visalberghi, & Ferrari 2009]. Social conformity effects related to this could be

470 important, for example, in explaining tendencies in birds [Catchpole & Slater, 2008; Lachlan,

471 Janik, & Slater, 2004], whales [Garland et al., 2011] and primates [Watson et al., 2015] for

472 vocal convergence among associating individuals. Whatever the underlying explanation for

473 the behavior we recorded in our vervet splinter groups, the strength of their inclination to

474 persist in the choice of the dietary option prevalent in their parent group despite their

475 knowledge of perfectly viable alternatives demonstrates a marked resilience in a primate

476 tradition documented in the wild.

477

478 **Acknowledgements**

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Figure legends:

Figure 1: a) Correlation between adult females' rank and the average number of minutes

spent eating the initially palatable color during experiments 1 to 6, for all females who

participated in all 6 trials. The black line represents the power trend line. Pink points represent

females from the two groups trained to eat pink (NH: blue line around data points, LT: black

line around data points), blue points represent females from blue trained groups (AK: black

line around data points, BD: pink line around data points). b) Time spent by each female

eating the initially palatable color for each group. Number in brackets next to name code

shows female's rank. Boxes around results highlight the reduced time spent feeding on the

preferred color by the lowest-ranking females of each group.

Figure 2: Map of the home ranges of two groups In Betweeners and Intaka that split from

Baie Dankie group.

Figure 3: Average percentage of minutes spent eating the preferred color ('local preference')

compared to the other color ('other') by individuals before (all recorded trials pre-fission

where the individuals participated) and after split (1st trial) from the original BD group: a) for

IB individuals; b) for IN individuals.

Figure 4: Average time (in minutes) spent eating the preferred color by low-ranking females

of NH, in the group context and when tested alone.

Figure 5: Average % of observed minutes eating maize of each color in both pink- and blue-

trained groups: a) females that tried aloe maize during the training phase (n=20); b) females

that never picked up a single maize piece treated with aloe (n=19).

726

727   **Figure 6:** a) Mean number of BD monkeys eating the preferred color (blue) and the

728   alternative color (pink) collected in 10-minute scans and expressed during the first two hours

729   in experiments 1-6. b) Mean cumulative number of BD monkeys eating the preferred color

730   (blue) and the alternative color (pink) across successive scan periods. Supplementary Fig. 6.

731   Mean cumulative number of BD monkeys eating the preferred color (blue) and the alternative

732   color (pink) across successive scan periods during the first two hours in Experiment 1.

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Highlights

- First report of group fission in vervets reveals high tradition resilience

- Initial group was trained to prefer one of two foods but low-rankers sampled non-preferred option

- After fission these monkeys ate only the parent group's preferred option

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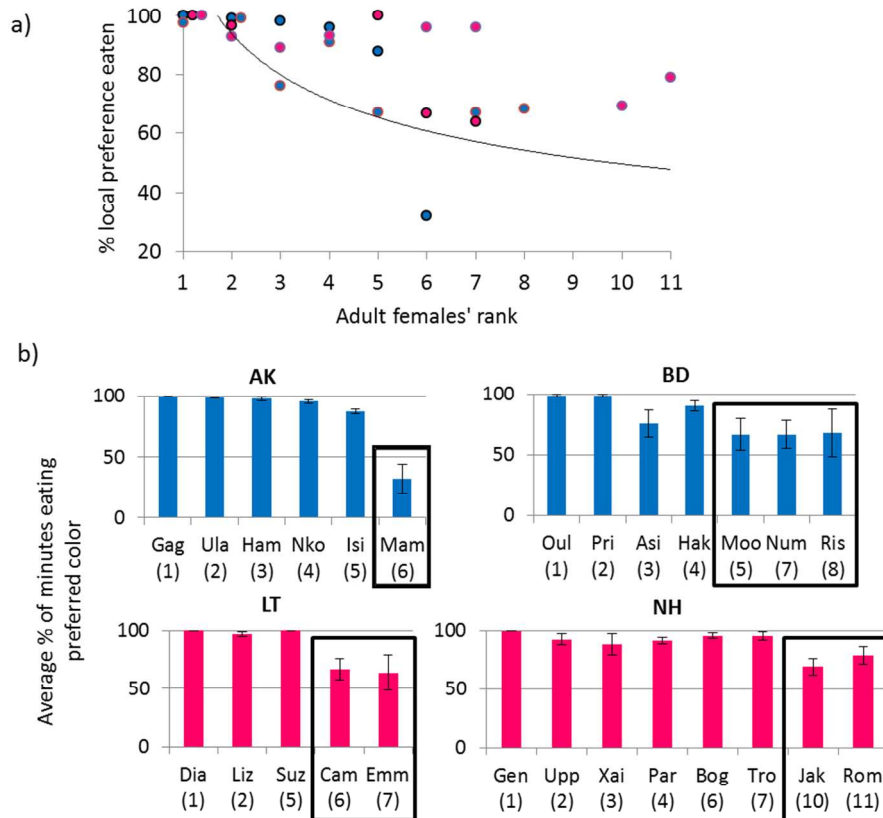55
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Fig. 1

Figure 1: a) Correlation between adult females' rank and the average number of minutes spent eating the initially palatable color during experiments 1 to 6, for all females who participated in all 6 trials. Pink points represent females from the two groups trained to eat pink (NH: blue line around data points, LT: black line around data points), blue points represent females from blue trained groups (AK: black line around data points, BD: pink line around data points). b) Time spent by each female eating the initially palatable color for each group. Number in brackets next to name code shows female's rank. Boxes around results highlight the reduced time spent feeding on the preferred color by the lowest-ranking females of each group.
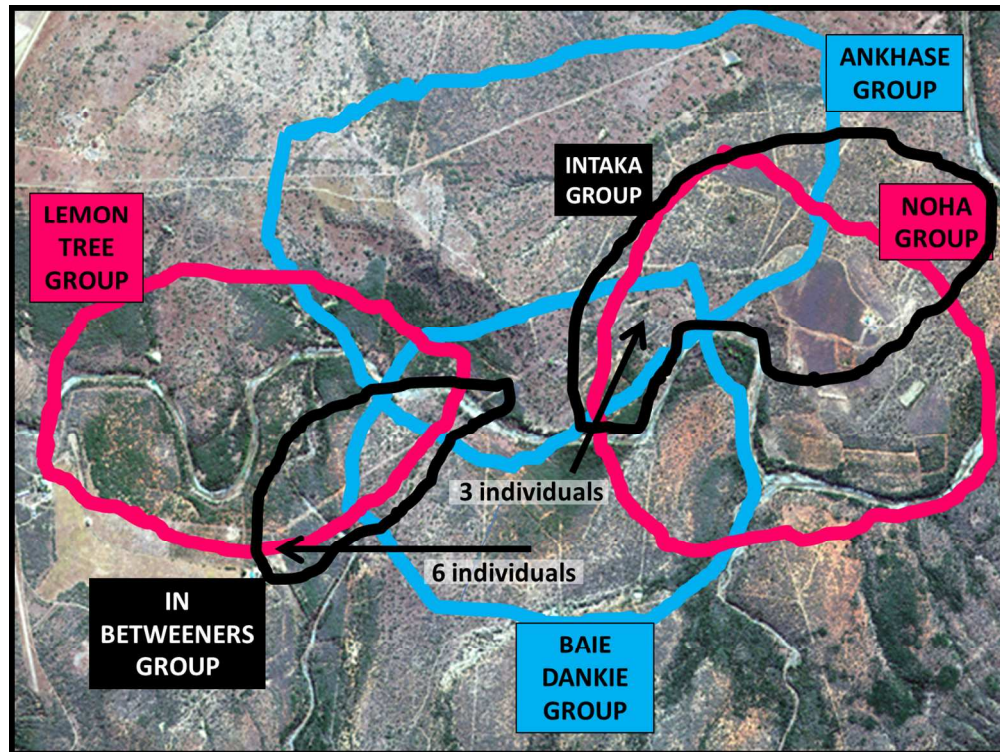
182x175mm (150 x 150 DPI)

Figure 2: Map of the home ranges of two groups IB and IT that split from BD.
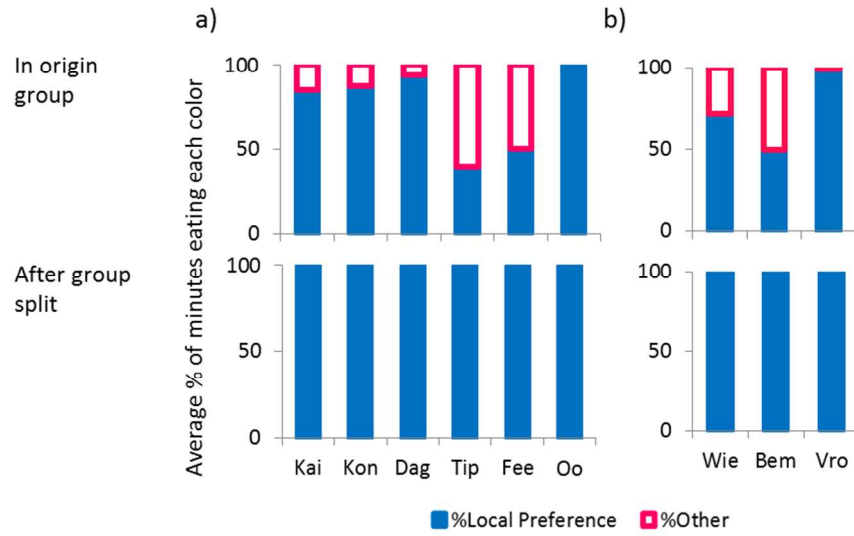
257x193mm (150 x 150 DPI)

Fig. 3

Figure 3: Average percentage of minutes spent eating the preferred color ('local preference') compared to the other color ('other') by individuals before (all recorded trials pre-fission where the individuals participated) and after split (1st trial) from the original BD group: a) for IB individuals; b) for IN individuals.

170x121mm (150 x 150 DPI)

Fig. 4

a)

In group
context

b)

Tested
alone

Average % of minutes eating each color

100
50
0

100
50
0

Pre   Zar   Bog   Tro   Lha   Jak   Rom
(F5) (F6) (F7) (F8) (F9) (F10)(F11)
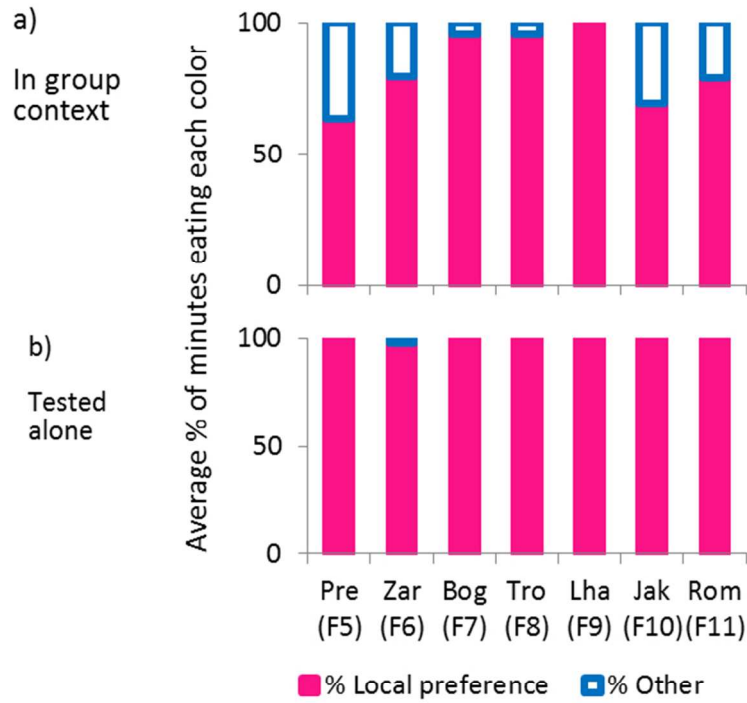
■ % Local preference □ % Other

Figure 4: Average time (in minutes) spent eating the preferred color by low-ranking females of NH, in the group context and when tested alone.

133x125mm (150 x 150 DPI)

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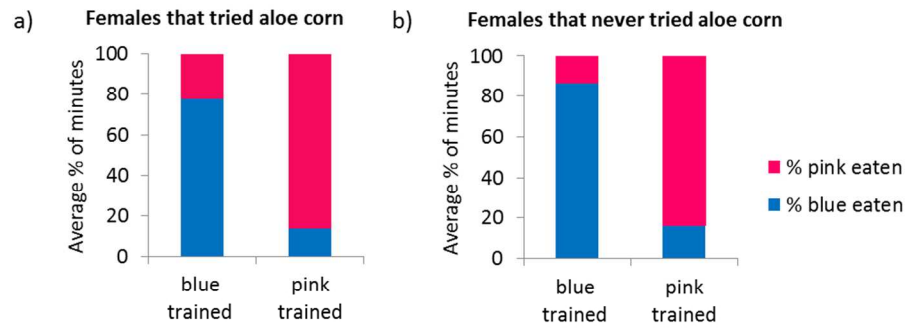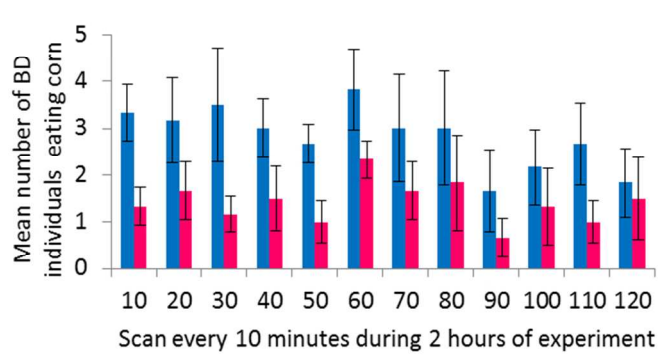54
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Fig. 5

Figure 5: Average % of observed minutes eating corn of each color in both pink- and blue-trained groups: a) females that tried aloe corn during the training phase (n=20); b) females that never picked up a single corn piece treated with aloe (n=19).

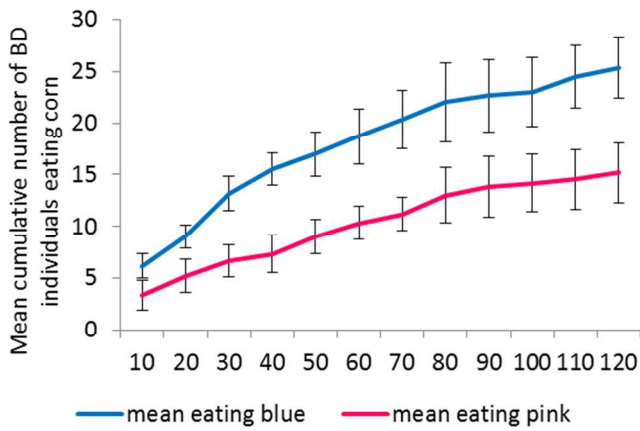190x93mm (150 x 150 DPI)

Fig. 6

a)

b)

Figure 6: a) Mean number of BD monkeys eating the preferred color (blue) and the alternative color (pink) collected in 10-minute scans and expressed during the first two hours in experiments 1-6. b) Mean cumulative number of BD monkeys eating the preferred color (blue) and the alternative color (pink) across successive scan periods.

153x166mm (150 x 150 DPI)

Table 1.

Composition of the two splinter groups

	ID code	Age	Sex	rank in BD
	Kai	AD	F	9
	Dag	AD	F	10
IB	Tip	AD	F	11
	Fee	JU3	F	>11
	Kon	JU2	F	9
	Oo	AD	M	3
	Wie	AD	F	9
IN	Bem	AD	F	10
	Vro	AD	F	11

Table footnote:

Group composition of the two groups split from 'Baie Dankie' (BD) group; name codes (2

letter for males, 3 for females), age class (AD=adult, JU= juvenile with age in years), sex

(F=female, M=male) and rank just before leaving BD (offspring have the rank of their

mother). 'In-Betweeners' (IB) last experiment in BD group was 19th June 2012; the

experiment after was 31st January 2013. 'Intaka' (IN) last experiment in BD group was 15th

December 2012 and test after split was 15th March 2014.

Table 2.

Number of minutes splinter group females spent eating (a) pink or (b) blue in their origin group before they split off, during each of the six test sessions and in total.

a)

TEST	1	2	3	4	5	6	total
Kai	-	2	-	3	-	-	**5**
Dag	-	-	0	2	-	-	**2**
Tip	-	1	4	6	-	-	**11**
Wie	-	-	-	4	-	10	**14**
Bem	-	-	-	5	-	14	**19**
Vro	-	-	-	0	0	4	**4**

b)

TEST	1	2	3	4	5	6	total
Kai	-	4	-	15	-	-	**19**
Dag	-	-	2	7	-	-	**9**
Tip	-	5	1	1	-	-	**7**
Wie	-	-	-	9	-	4	**13**
Bem	-	-	-	2	-	2	**4**
Vro	-	-	-	22	12	28	**62**